The Effects of Prediction Error on Episodic Memory

Dissertation

zur Erlangung des Doktorgrades

der Naturwissenschaften

vorgelegt beim Fachbereich 05 Psychologie und Sportwissenschaften

der Johann Wolfgang Goethe-Universität

in Frankfurt am Main

von

Gözem Turan

aus Ankara (Turkey)

Frankfurt 2023

(D 30)

Vom Fachbereich 05 der

Johann Wolfgang Goethe-Universität als Dissertation angenommen.

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Datum der Disputation: 19.12.2023

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“But, of course, memory and responsibility are strangers. They're foreign to each other. Memory always goes its own way quite regardless.”

— Ali Smith, Autumn

“‘We dissect flies,’ answered the philosopher. ‘We measure lines. We study numbers. We agree on two or three points which we understand, and we disagree on two or three thousand which we don’t understand.’”

— Voltaire, Micromegas

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Summary

Understanding the brain's proactive nature and its ability to anticipate the future has been a longstanding pursuit in philosophy and scientific research. The predictive processing framework explains how the brain generates predictions based on environmental regularities and adapts to both predicted and unpredicted events. Prediction errors (PE) occur when sensory evidence deviates from predictions, triggering cognitive and neural processes that enhance learning and subsequent memory. However, the effects of PE on episodic memory have not been clearly explained. This dissertation aims to address three key questions to advance our understanding of PE and episodic memory. First, how does the degree of PE influence episodic memory, and how do expected and unexpected events interact in this process? Second, what insights can be gained from studying the electrophysiological activity associated with prediction violations, and what role does PE play in subsequent memory benefits? Lastly, how do memory processes change across the lifespan, and how does this impact the brain's ability to remember events? By answering these questions, this dissertation contributes to advancing our understanding of the cognitive and neural mechanisms underlying the relationship PE and episodic memory.

Study 1 investigated the impact of varying levels of PEs on episodic memory. Two experiments were conducted using different stimuli and designs. In Experiment 1, participants learned associations between cue-target pairs related to musical instrument sounds and object categories. In Experiment 2, participants learned associations between artificial creatures called "Wubbels" and environmental categories. Both experiments consisted of prediction learning, encoding, and recognition phases. The results showed that participants successfully generated predictions and exhibited increasing accuracy rates. The manipulation of PE levels was confirmed, with participants rating high PE trials as having the highest discrepancy between predicted and presented categories. However, contrary to the hypothesis, the U-shaped effect of PE on memory was not observed. Instead, a memory advantage was consistently found for low PE trials. The findings suggest a memory congruency effect, indicating that memory performance is better when the predicted and presented information align. The absence of a memory benefit for high PE trials suggests that additional factors and task sensitivity may influence the role of PE in facilitating improved memory.

Study 2 examined the effects of PE on episodic memory and the companying cognitive processes using event-related potentials (ERPs). The study involved a three-day experiment. On the first two days, participants implicitly learned object pairs presented sequentially. On the

third day, new objects were introduced, either violating the expected item (violation items) or serving as a baseline (non-violation items). Item recognition memory and associative memory were tested. The results indicated that participants successfully learned the object pairs and exhibited faster reaction times for the second item of the pair, suggesting prediction learning. However, there were no significant differences in memory performance between violation and non-violation items. Despite the lack of behavioral effects, the neural correlates analysis revealed a significant relationship between the recollection component and item recognition memory for violated items. Higher amplitude values were observed for remembered violation items compared to forgotten violation trials. The familiarity component did not show a significant effect of PE, and there was no relationship between the P3 amplitude and subsequent memory. These findings suggest that recollection plays a crucial role in the interplay between PE and episodic memory. The study provides valuable insights into the complex nature of PE and its relationship with memory processes, emphasizing the importance of deviations from expectations in generating a stronger recollection signal and potentially facilitating better subsequent memory.

Study 3 investigated the effects of PE on episodic memory across different age groups, specifically children, younger adults, and older adults. The study utilized a statistical learning paradigm similar to Study 2, where participants learned object pairs over two days and their memory was tested on the third day, including violation items (presented after the first item of a pair) and non-violation items (presented between pairs). Response rates and classification indices were calculated as behavioral measures. The results showed that there was no memory enhancement effect of PE in any of the age groups. Contrary to expectations, children exhibited better classification for non-violating similar items compared to violating similar items. This finding suggests that children may remember non-violation items in greater detail, challenging the assumption that PE consistently facilitates episodic memory. The observed memory advantages for non-violation similar items in children highlight the importance of exploring additional factors that may impact memory processes. The study did not find robust evidence supporting the role of PE in modulating episodic memory across the lifespan.

In conclusion, the three studies presented in this dissertation did not find a subsequent memory advantage for events that violated predictions, strongly indicating that the effects of PE on episodic memory is not as straightforward and consistent as previously postulated. Even though our carefully designed experiments to isolate and manipulate PE indicated that participants effectively generated violations of predictions, these violations did not translate into improved memory performance. This challenges the previous assumption that PE reliably improves memory performance. Nevertheless, the dissertation has provided valuable insights into several crucial aspects related to the interplay between PE and episodic memory. First, Study 1 revealed that events in line with our predictions were remembered better compared to events eliciting PE. This suggests that conforming to expectations may have a positive impact on memory encoding. Study 2 emphasized the significance of the recollection component as a potential moderator in the relationship between PE and episodic memory. Higher recollection component amplitude was observed for remembered violation trials, indicating that the violation of expectations can enhance the recollection process. Study 3 uncovered an intriguing finding that children exhibited more specific memory for non-violation items compared to violation items. This suggests that children may show increased pattern separation and a better ability to differentiate similar lures when the items do not violate the expected structure.

Overall, these insights contribute to a deeper understanding of the complex interplay between PE and episodic memory. The results challenge the notion that PE consistently drives new learning and improves memory, highlighting the need for further investigation and consideration of factors that influence the impact of PE on memory processes.

The dissertation concludes with a comprehensive discussion that explores additional modulating factors influencing the interaction between PE and episodic memory. It delves into methodological and theoretical considerations to further elucidate the topic. The discussion also encompasses an exploration of the neural correlates associated with the processing of PE and its potential enhancing effect on episodic memory. Furthermore, it investigates possible explanations for the intriguing finding that children exhibited better memory for details of non-violation items. The limitations of the studies are identified, and future research directions are proposed. Lastly, the dissertation offers a broad perspective on the interplay between PE and episodic memory, highlighting the need for continued exploration and investigation in this field.

German Summary

Das Verständnis der proaktiven Natur des Gehirns und seiner Fähigkeit, die Zukunft vorauszusehen, ist ein langjähriges Bestreben der Philosophie und der wissenschaftlichen Forschung. Das Konzept der prädiktiven Verarbeitung erklärt, wie das Gehirn auf der Grundlage von Regelmäßigkeiten in der Umwelt Vorhersagen trifft und sich sowohl an vorhergesagte als auch an nicht vorhergesagte Ereignisse anpasst. Vorhersagefehler (VF) treten auf, wenn die sensorische Evidenz von den Vorhersagen abweicht. Sie lösen kognitive und neuronale Prozesse aus, die das Lernen und das anschließende Gedächtnis verbessern. Die Auswirkungen von VF auf das episodische Gedächtnis sind jedoch noch nicht eindeutig geklärt. In dieser Dissertation sollen drei zentrale Fragen beantwortet werden, um unser Verständnis von VF und episodischem Gedächtnis zu verbessern. Erstens: Wie beeinflusst das Ausmaß von VF das episodische Gedächtnis, und wie interagieren erwartete und unerwartete Ereignisse in diesem Prozess? Zweitens: Welche Erkenntnisse lassen sich aus der Untersuchung der elektrophysiologischen Aktivität im Zusammenhang mit VF gewinnen, und welche Rolle spielen VF bei späteren Gedächtnisleistungen? Und schließlich: Wie verändern sich Gedächtnisprozesse über die Lebensspanne hinweg, insbesondere in Bezug auf VF und ihre Interaktion mit dem episodischen Gedächtnis, und wie wirkt sich dies auf die Fähigkeit des Gehirns aus, sich an Ereignisse zu erinnern? Durch die Beantwortung dieser Fragen trägt diese Dissertation dazu bei, unser Verständnis der kognitiven und neuronalen Mechanismen, die der Beziehung zwischen VF und episodischem Gedächtnis zugrunde liegen, zu verbessern.

Studie 1 untersuchte die Auswirkung unterschiedlicher eVF-Stärken auf das episodische Gedächtnis. Es wurden zwei Experimente mit unterschiedlichen Stimuli und Designs durchgeführt. In Experiment 1 lernten die Teilnehmenden Assoziationen zwischen Hinweisreiz-Zielreiz-Paaren, die sich auf Musikinstrumentenklänge und Objektkategorien bezogen. In Experiment 2 lernten die Teilnehmenden Assoziationen zwischen künstlichen

Kreaturen namens "Wubbels" und Umweltkategorien. Beide Experimente bestanden aus Vorhersage-Lern-, Enkodierungs- und Wiedererkennungsphasen. Die Ergebnisse zeigten, dass die Teilnehmenden erfolgreich Vorhersagen generierten und dabei eine zunehmende Genauigkeit aufwiesen. Die Manipulation des VF-Niveaus wurde bestätigt, wobei die Teilnehmenden bei Versuchen mit hohem VF die größte Diskrepanz zwischen den vorhergesagten und den präsentierten Kategorien feststellten. Entgegen der Hypothese wurde jedoch kein U-förmiger Effekt von VF auf das Gedächtnis beobachtet. Stattdessen wurde durchweg ein Gedächtnisvorteil für die Bedingung mit niedrigem VF festgestellt. Die Ergebnisse deuten auf einen Gedächtniskongruenzeffekt hin, der besagt, dass die Gedächtnisleistung besser ist, wenn die vorhergesagten und präsentierten Informationen übereinstimmen. Das Fehlen eines Gedächtnisvorteils bei der Bedingung mit hohem VF lässt vermuten, dass zusätzliche Faktoren und die Aufgabensensitivität die Rolle von VF bei der Verbesserung des Gedächtnisses beeinflussen könnten.

Studie 2 untersuchte die Auswirkungen von VF auf das episodische Gedächtnis und die begleitenden kognitiven Prozesse anhand ereigniskorrelierter Potenziale (EKPs). Die Studie umfasste ein dreitägiges Experiment. An den ersten beiden Tagen lernten die Teilnehmenden implizit Objektpaare, die nacheinander präsentiert wurden. Am dritten Tag wurden neue Objekte eingeführt, die entweder gegen das erwartete Objekt verstießen (Objekte mit VF) oder dies nicht taten und damit als Ausgangswert dienten (Objekte ohne VF). Das Wiedererkennungsgedächtnis und das assoziative Gedächtnis wurden getestet. Die Ergebnisse zeigten, dass die Teilnehmenden die Objektpaare erfolgreich lernten und schnellere Antwortzeiten für das zweite Objekt des Paares aufwiesen, was auf ein Vorhersage-Lernen schließen lässt. Es gab jedoch keine signifikanten Unterschiede in der Gedächtnisleistung zwischen Objekten mit und ohne VF. Trotz des Fehlens von Verhaltenseffekten ergab die Analyse der neuronalen Korrelate eine signifikante Beziehung zwischen der

Erinnerungskomponente und dem episodischen Gedächtnis für Objekte mit VF. Es wurden höhere Amplitudenwerte für erinnerte Objekte mit VF im Vergleich zu vergessenen Objekte mit VF beobachtet. Die Vertrautheitskomponente zeigte keine signifikante Auswirkung des VF, und es gab keine Beziehung zwischen der P3-Amplitude und der nachfolgenden Erinnerung. Diese Ergebnisse legen nahe, dass der Abruf eine entscheidende Rolle im Zusammenspiel zwischen VF und episodischem Gedächtnis spielt. Die Studie liefert wertvolle Einblicke in die komplexe Natur dees VF und seiner Beziehung zu Gedächtnisprozessen und unterstreicht die Bedeutung von Abweichungen von den Erwartungen für die Erzeugung eines stärkeren Erinnerungssignals und die mögliche Erleichterung einer besseren späteren Erinnerung.

Studie 3 untersuchte die Auswirkungen von VF auf das episodische Gedächtnis in verschiedenen Altersgruppen, insbesondere bei Kindern, jüngeren Erwachsenen und älteren Erwachsenen. In der Studie wurde ein statistisches Lernparadigma ähnlich wie in Studie 2 verwendet, bei dem die Teilnehmenden an zwei Tagen Objektpaare lernten und ihr Gedächtnis am dritten Tag getestet wurde, einschließlich der Objekte, die gegen die Regeln verstießen (die nach dem ersten Objekt eines Paares präsentiert wurden), und der Objekte, die nicht gegen die Regeln verstießen (die zwischen den Paaren präsentiert wurden). Als Verhaltensmaßzahlen wurden Antwortraten und Klassifikationsindizes berechnet. Die Ergebnisse zeigten, dass VF in keiner der Altersgruppen eine gedächtnisfördernde Wirkung hatte. Entgegen den Erwartungen zeigten die Kinder eine bessere Klassifizierung für ähnliche Objekte ohne VF als für ähnliche Objekte mit VF. Dieser Befund deutet darauf hin, dass sich Kinder an Objekte ohne VF detaillierter erinnern können, was die Annahme in Frage stellt, dass VF durchweg das episodische Gedächtnis fördert. Die beobachteten Gedächtnisvorteile für ähnliche Objekte ohne VF bei Kindern unterstreichen die Bedeutung der Erforschung zusätzlicher Faktoren, die Gedächtnisprozesse beeinflussen können. In der Studie wurden keine stichhaltigen Belege für die Rolle von VF bei der Modulation des episodischen Gedächtnisses über die gesamte Lebensspanne hinweg gefunden.

Zusammenfassend lässt sich sagen, dass die drei in dieser Dissertation vorgestellten Studien keinen nachträglichen Gedächtnisvorteil für Ereignisse ergaben, die Vorhersagen verletzten, was stark darauf hindeutet, dass die Auswirkungen von VF auf das episodische Gedächtnis nicht so einfach und konsistent sind wie bisher postuliert. Obwohl unsere sorgfältig konzipierten Experimente zur Isolierung und Manipulation von VF darauf hinwiesen, dass die Teilnehmenden tatsächlich Vorhersageverletzungen erlebten, führten diese Verletzungen nicht zu einer verbesserten Gedächtnisleistung. Dies stellt die bisherige Annahme in Frage, dass VF die Gedächtnisleistung zuverlässig verbessert. Nichtsdestotrotz hat die Dissertation wertvolle Einblicke in mehrere entscheidende Aspekte im Zusammenhang mit dem Zusammenspiel von VF und episodischem Gedächtnis geliefert. Erstens zeigte Studie 1, dass Ereignisse, die unseren Vorhersagen entsprachen, besser erinnert wurden als Ereignisse, die VF auslösten. Dies deutet darauf hin, dass die Übereinstimmung mit den Erwartungen einen positiven Einfluss auf die Gedächtnisenkodierung haben kann. In Studie 2 wurde die Bedeutung der Erinnerungskomponente als potenzieller Moderator für die Beziehung zwischen VF und episodischem Gedächtnis hervorgehoben. Eine höhere Amplitude der Erinnerungskomponente wurde bei Objekten mit VF beobachtet, was darauf hindeutet, dass die Verletzung von Erwartungen den Erinnerungsprozess verbessern kann. In Studie 3 wurde die interessante Erkenntnis gewonnen, dass Kinder ein spezifischeres Gedächtnis für Objekte ohne VF im Vergleich zu Objekten mit VF aufwiesen. Dies deutet darauf hin, dass Kinder möglicherweise eine verstärkte Tendenz zu stark unterscheidbaren Gedächtnisspuren und eine bessere Fähigkeit zur Unterscheidung ähnlicher Objekte zeigen, wenn die Objekte nicht gegen die erwartete Struktur verstoßen.

Insgesamt tragen diese Erkenntnisse zu einem tieferen Verständnis des komplexen Zusammenspiels zwischen VF und episodischem Gedächtnis bei. Die Ergebnisse stellen die Vorstellung in Frage, dass VF durchgängig neues Lernen fördert und das Gedächtnis verbessern, und unterstreichen die Notwendigkeit weiterer Untersuchungen und Überlegungen zu Faktoren, die die Auswirkungen von VF auf Gedächtnisprozesse beeinflussen.

Die Dissertation schließt mit einer umfassenden Diskussion, in der weitere modulierende Faktoren untersucht werden, die die Interaktion zwischen VF und episodischem Gedächtnis beeinflussen. Sie geht auf methodische und theoretische Überlegungen ein, um das Thema weiter zu erhellen. Die Diskussion umfasst auch eine Untersuchung der neuronalen Korrelate, die mit der Verarbeitung von VF und ihrer potenziell verstärkenden Wirkung auf das episodische Gedächtnis verbunden sind. Darüber hinaus werden mögliche Erklärungen für das verblüffende Ergebnis untersucht, dass Kinder ein besseres Gedächtnis für Details von Objekten ohne VF aufwiesen. Die Grenzen der Studien werden aufgezeigt, und es werden künftige Forschungsrichtungen vorgeschlagen. Schließlich bietet die Dissertation eine umfassende Perspektive auf die komplizierte Dynamik zwischen VF und episodischem Gedächtnis und unterstreicht den Bedarf an fortgesetzter Erforschung und Untersuchung in diesem Bereich.

1. Theoretical Background

Understanding the principles of the brain and its interaction with the environment has been a longstanding pursuit in various philosophical and scientific research. One fundamental principle regarding the brain is its proactive nature and its ability to anticipate the future (Bar, 2007; Friston, 2010). The predictive coding framework, which has gained recent attention, proposes that the brain works as a prediction machine, aiming to minimize surprise and adapt to the complexities of the environment. This is achieved through hierarchically organized cognitive systems that compare predictions with sensory inputs from the environment (Clark, 2013; Heilbron & Chait, 2018; Knill & Pouget, 2004). When incoming sensory evidence deviates from predictions, it results in prediction error (PE), which is then processed and passed up the hierarchy to update internal models, thus improving predictions over time (Bar, 2007). Moreover, the degree of PE initiates cognitive and neural processes that enhance learning, related to the subsequent memory (Henson & Gagnepain, 2010). Yet, the effects of PE on episodic memory, as compared to learning from regularities, have been comparatively underexplored.

The predictive coding framework thus suggests that our brain utilizes past experiences to anticipate and prepare for the future. To gain a better understanding of these processes and their impact on episodic memory, the presented dissertation addressed three key questions:

1. How does the degree of PE affect episodic memory, how do expected and unexpected[1] events interact in the process of episodic memory?
2. What insights can be derived from the electrophysiological activity associated with the violation of predictions regarding the relationship between PE and episodic memory, and what role does PE play in subsequent memory benefits?
3. What can we[2] learn about changes in the processes of PE as we age, how does this knowledge improve our understanding of the brain's ability to remember events over the lifespan?

These inquiries can contribute to advancing our comprehension of the cognitive and neural mechanisms underlie the processes of PE as a fundamental brain function and its significance in supporting episodic memory. With this aim, three studies that all aimed at

[1] Even though we are aware of the conceptual differences among the terms, for the ease of readability, the term expectation will be utilized to refer prediction, while violation of predictions will be employed interchangeably with PE. For a more comprehensive overview of various forms of novelty, please refer to Quent et al. (2021).
[2] The inclusive pronoun 'we' is utilized throughout the entire work instead of the singular pronoun 'I'.

examining the interplay between PE and episodic memory were conducted. In the following sections, the theoretical background for the presented work will be provided. Chapter 1 presents the predictive account of episodic memory, with a particular focus on the varying levels of PE and their impact on subsequent memory. This chapter addresses the gaps in the current literature and highlights the need for further investigation. Chapter 2 comprises the electrophysiological correlates of PE, which emphasizes the importance of understanding the neural underpinnings of the interplay between PE and memory benefits. The chapter explores the relationship between PE and neural activity to shed light on the mechanisms involved. Chapter 3 takes a lifespan perspective on the prediction account of memory and motivates the investigation of age-related changes in memory processes and their interaction with PE. This chapter examines how memory processes change across the lifespan and how they interact with PE across different stages of life. Finally, the present findings are integrated into a larger research context, and their implications are discussed, along with limitations that should be acknowledged.

1.1. Predictive Account of Episodic Memory

Episodic memory refers to the cognitive ability of remembering specific events from one's personal past (Tulving, 197(Tulving, 2012). It involves encoding, storage and retrieving details such as the time, place, and context in which the specific event occurred (Underwood, 1969). Its function includes binding details belonging to the same event while separating them from other details associated with different events (O'Reilly & Norman, 2002) Zimmer et al., 2006). Broadly speaking, research on episodic memory investigates its behavioral and neural mechanisms and seeks to understand why some events are more memorable than others. To comprehend the factors influencing event memorability, for example, the predictive processing framework (Bar, 2007; Friston, 2010; Knill & Pouget, 2004) suggests that events deviating from our expectations are better remembered compared to those aligning with them.

The predictive processing framework (Bar, 2007; Friston, 2010; Knill & Pouget, 2004) elucidates how the brain generates predictions based on environmental regularities and adapts itself to both predicted and unpredicted events. Given the importance of performing efficiently and being functional in daily life, it becomes necessary to extract statistical regularities from the environment and continually update the predictions to account for conflicts between established regularities and incoming sensory input. The framework suggests that remembering and learning from PEs improve future predictions. In other words, the ability to encode and retrieve PEs contributes to better anticipation and adaptation to complex and ever-changing environments.

1.1.1. Memory-Enhancement for PE and Memory Congruency Effect

Several recent studies have examined the relationship between PE and memory processes, aiming to elucidate the mechanisms underlaying memory-enhancing effects of PE (Bein et al., 2021; Brod et al., 2018; Greve et al., 2017; Kafkas & Montaldi, 2018; Ortiz-Tudela et al., 2023; Quent et al., 2022; Rouhani et al., 2020; Wahlheim et al., 2022). These studies typically involve an encoding phase where PE occurs, followed by a subsequent memory phase. Consistent with the predictive processing framework, it has been observed that events giving rise to PE are often better remembered due to the encoding of detailed snapshots of these events (Henson & Gagnepain, 2010). Furthermore, it has been proposed that events that violate our predictions are encoded as distinct memory traces, separate from those those related to previous predictions, without disrupting our existing predictions (Frank et al., 2020). Thus, the new information provided by PE is integrated into memory alongside existing predictions, allowing the ability to update predictions by incorporating unexpected elements while preserving the coherence of our existing predictions.

On the contrary, an alternative line of research, known as the memory congruency effect, points that events aligning with our predictions are also better remembered (Alba & Hasher, 1983; Anderson, 1981; Craik & Tulving, 1975). For instance, congruent associations tend to exhibit better memory compared to incongruent associations. Recent behavioral studies have provided substantial support for this notion, such as research involving pairs of items and scenes (Brod & Shing, 2019; Liu et al., 2018; Ortiz-Tudela et al., 2017; van Kesteren et al., 2013), pairs of items and locations (Atienza et al., 2011), and non-preexisting relations (Ostreicher et al., 2010). In summary, research indicates that both events eliciting PE and events aligning with our predictions can lead to enhanced memory performance.

1.1.2. The U-Shape Function of PE on Memory

When considering the lines of research, namely memory-enhancement for PEs and memory congruency effects, two key questions arise: (i) how do different levels of PE affect memory, and (ii) how do expected and unexpected events compete in memory processes? To address these questions, the Schema-Linked Interactions between Medial Prefrontal and Medial Temporal Lobe Model (SLIMM, Van Kesteren et al., 2012) proposed a U-shaped relationship between PE and memory, involving the collaboration of different brain systems. According to the model, the process of generating predictions and subsequent memory operations consists of several stages. First, when encountering an event, relevant information from memory is activated, which assumingly reinstates perceptual traces and facilitates consolidation. This process is aided by the hippocampus via pattern completion, which involves the reinstatement of information based on partial cues. Thus, the related representation of the entire event is activated upon exposure. The generated prediction is then compared to the sensory input, resulting in the computation of PE at varying levels. These levels of PE influence subsequent cognitive and neural processes. Specifically, events with low or high levels of PE are better remembered compared to those with medium levels. Low PEs are associated with increased activity in the medial prefrontal cortex (mPFC), which strengthens existing connections underlying predictions and facilitates future information at retrieval. Conversely, events generating high PE enhance learning and memory through the involvement of the medial temporal lobe (MTL), which creates snapshots of these events, resulting in memory advantage. Events that are neither strongly predicted nor unpredicted do not benefit memory since the activation of mPFC and MTL is weak. In summary, varying levels of PE, ranging from low to high, are expected to demonstrate a U-shaped relationship with episodic memory: events generating low and high PEs are better remembered compared to events with medium levels.

The U-shaped relationship between PE and episodic memory has received support from recent research (Greve et al., 2018; Quent et al., 2022). In one study, Greve and colleagues (2018) conducted experiments where participants learned a rule regarding the pairing of object exemplars. This rule was then manipulated at three levels: congruent, incongruent, and unrelated, based on the strength of their relatedness to previously learned associations. The congruent level maintained the rule, while the incongruent level reserved it. In the unrelated level, the rule changed after the first trial, with no specific rule established. These rules were violated or confirmed on critical trials just before testing memory performance. The results indicated the U-shape relationship between PE levels and memory, with worse memory performance observed for the unrelated level compared to congruent and incongruent levels. However, it is important to note that the poorer memory observed for the medium level might be attributed to the need to create new associations rather than representing the medium level within the overall spectrum for PE. To address the issue of the continuous spectrum for PE, Quent et al. (2022) conducted a virtual reality study. Participants were immersed in a virtual kitchen where kitchen objects were positioned in different locations, each varying in degrees of congruency based on semantic predictions. For instance, a kettle placed on the counter would be predicted (i.e., low PE), a kettle on the table would be neither strongly predicted nor unpredicted (i.e., medium PE), and a kettle near the trash can would be unpredicted (i.e., high PE). Memory for the object-location pairs was tested using free recall and an alternative forced-choice task. The results aligned with the U-shaped function of PE on memory, indicating a memory advantage for predicted and unpredicted object-location pairs compared to the medium level. However, it remains unclear how the U-shaped function operates when predictions are derived from an episodic context rather than relying on pre-experimental knowledge.

1.1.3. Interim Summary

Although given the importance of these studies providing evidence for the U-shape function of PE on memory (Greve et al., 2018; Quent et al., 2022), further investigation is required to explore the role of PE with a medium level in the context of episodic memory. A significant gap exists in the research concerning the medium level of prediction. This level holds importance in the spectrum as its memory performance compared to the other levels to draw conclusions, representing a state where predictions are neither violated nor confirmed. However, previous studies either lacked a medium level (Bein et al., 2021; Kafkas & Montaldi, 2018) or had a medium level that was unrelated to the previously induced prediction learning (Greve et al., 2018). Therefore, to address this gap in the literature, it is essential to examine the U-shaped function of PE on memory, specifically with a medium level directly associated with previously induced prediction learning. This approach facilitates a comprehensive understanding of the impact of PE on episodic memory across the prediction spectrum, including a comparable medium level, and provides valuable insights into this process.

- Recent research has identified two main factors that impact subsequent memory performance: the memory benefit for PE and memory congruency effect.
- The U-shaped function of PE has been proposed, with both low and high levels of PE resulting in better memory performance compared to medium levels.
- However, previous studies investigating the effect of PE on episodic memory have lacked a comparable medium level of PE that is related to previously induced prediction learning.
- Therefore, it is crucial to study the full range of PE to fully understand the interplay between PE and subsequent memory performance.
- **Dissertation aim 1:** Testing the U-shape relationship between PE and episodic memory.

1. 2. The Electrophysiological Correlates of PE and Episodic Memory

To understand how memory works, implementing behavioral measures with neuroimaging techniques is crucial (Ranganath, 2022). Given the nature of PE processing, which involves an explicit evaluation of events, relying solely on behavioral measures may not capture its underlying components. Electrophysiological measures enable us to investigate data on a trial-by-trial basis. By comparing the electrophysiological changes in time-locked to the events that generate PE, we can gain deeper insights into how the brain processes PE and underlying mechanisms that enhance memory performance. Currently, there is limited knowledge regarding the neural basis of the effects of PE on episodic memory.

Electroencephalography (EEG) is one of the widely employed neuroimaging tools that involves recording the brain's electrophysiological activity through electrodes placed on the scalp. It allows monitoring various cognitive processes with a high temporal resolution. The Event-related Potentials (ERPs) are derived from the EEG signal by extracting and averaging the neural responses that are time-locked to specific events. Researchers have been using the distinct components observed in the ERP waveforms to associate these components with specific cognitive processes or stages of information processing (Luck, 2014). In this dissertation, it is proposed that the ERPs can provide a precise and objective measure of neural activity associated with encoding and retrieval of events eliciting PE.

1.2.1. The Electrophysiological Correlates During Encoding

The investigation of novelty processing has a longstanding tradition in ERP research[3],[4]. For instance, one widely used experimental design in this domain is the oddball paradigm, which allows for a comparison of ERPs elicited by unexpected and expected stimuli. Among the ERP components that have been studied extensively within the oddball paradigm, the P3 component stands out. It is typically a positive deflection in the signal occurring around 300 – 500 ms after the stimuli presentation. Numerous studies have consistently demonstrated that the P3 component exhibits higher amplitude and displays a distinct scalp distribution in response to unexpected stimuli as compared to expected stimuli (Donchin, 1981; Friedman et al., 2001; Linden, 2005; Polich, 2007).

Prior research has shown that context-driven expectations influence the amplitude of P3 component (Cycowicz & Friedman, 2007; Schomaker et al., 2014; Schomaker & Meeter, 2018). That is, expectations about upcoming stimuli can significantly impact their processing. For instance, when participants anticipate encountering complex and novel stimuli, the P3 novelty effect, which reflects unexpectedness, diminishes compared to situations where no expectations are formed, irrespective of stimulus complexity. This implies that the presence of expectations reduces the extent of unexpectedness elicited by novel stimuli, consequently resulting in a reduced P3 response. These findings highlight the influential role of expectations in shaping the processing of novel information, as reflected in differences in P3 amplitude.

In addition to its involvement in expectancy processing, the P3 component has been investigated in relation to reward PE (as demonstrated in a recent meta-analysis by Stewardson and Sambrook (2020)) and with hierarchical violations (Vidal-Gran et al., 2020) as suggested by the predictive coding theory (Clark, 2013; Heilbron & Chait, 2018; Knill & Pouget, 2004). Previous studies (Stewardson & Sambrook, 2020; Vidal-Gran et al.,2020) have revealed that events giving rise to PE are encoded more effectively, leading to improved memory. However, no previous research has yet examined the electrophysiological correlates of PE together with its influence on episodic memory. It is still unclear whether P3 elicited by violations contributes to the subsequent memory of events that violate these predictions. Our study aims to bridge this

[3] Various ERP studies have investigated novelty processing and have identified different components such as mismatch negativity (MMN), N2, and N400. Although we acknowledge their importance for the literature, these components are beyond the scope of the present work.
[4] Unlike P3, MMN is associated with unattended deviants and involuntary orienting response (Friedman et al., 2001). Based on our understanding of PE, its processing is dynamic and requires an active evaluation of deviants. Therefore, although we are aware of the importance of the MMN in the Predictive Coding Framework (Baldeweg, 2007; Wacongne et al., 2012), this component is out of our scope.

gap in the literature by investigating the relationship between PE, P3 and subsequent memory, thereby advancing our understanding of the intricate interplay between PE and episodic memory.

1.2.2. The Electrophysiological Correlates During Retrieval

In terms of the ERP components regarding the retrieval, the dual process theories of recognition (Curran & Cleary, 2003; Jacoby, 1991; Mandler, 1980; Yonelinas, 2002, for a review Cowell et al., 2019) revealed that there are two distinct cognitive processes which contribute to episodic memory retrieval: familiarity and recollection. Familiarity refers a relatively undifferentiated feeling of having experienced the previous evet before, without recalling specific contextual and encoding details, whereas recollection involves a clear and distinct experience of contextual encoding details of an event (Doidge et al., 2017; Isingrini et al., 2016). The studies showed that familiarity and recollection have distinct patterns in scalp distribution, amplitude, and latency. Familiar items elicit a negative-going response, which is higher in amplitude between 300 – 500 ms at frontal electrodes. On the other hand, recollected items produce a positive-going response, which is higher in amplitude between 400 – 800 ms after the stimulus onset (Curran & Cleary, 2003).

Previous research showed that the effects of PE on memory are not limited to the encoding but also extended to retrieval process, for instance, Kafkas and Montaldi (2018) asked their participants to learn associations between symbols and object categories, which were then violated during encoding or retrieval. They employed a remember/know procedure to assess memory performance, requiring participants to judge if presented objects had been seen before or not. This procedure aimed to examine memory retrieval processes: familiarity and recollection. The findings revealed that unexpected objects improved recollection memory performance, conversely, expected objects enhanced familiarity performance. This suggests that the assessment of PE plays a vital role in facilitating subsequent retrieval mechanisms. Furthermore, the selective retrieval process (Lu et al., 2022) also proposes that error signals originating from PE may contribute to subsequent recollection during retrieval (Fenerci & Sheldon, 2022; Wahlheim et al., 2022). However, the neural processes underlying differences during retrieval of predicted and unpredicted events have not been understood well, yet. The aim of this dissertation was to establish a connection between the findings from electrophysiological and behavioral studies to shed light on the underlying neural processes involved in how PE affects episodic memory.

1.2.3. Interim Summary

Taken together, ERPs offer a precise and objective measure of neural activity associated with the processing of PEs. The preceding evidence highlights the significance of encoding and retrieval processes in the memory enhancement effect of PE. However, the specific electrophysiological correlates of these processes have not been directly investigated directly within the same experiment. To fill this research gap, the present dissertation aimed to investigate the relationship between PE, its ERP components, and memory within a single paradigm. Investigating the ERPs as an online measure of PE can significantly advance our understanding of the neural basis underlying the effects of PE on episodic memory.

- Previous EEG research has provided evidence that expected and unexpected events are processed differently in the brain, as indexed by P3 amplitude.
- However, no previous studies have examined the relationship between PE and its temporal correlates together with its effect on subsequent memory.
- Two distinct neural processes for familiarity and recollection play a role in PE retrieval: predicted events enhance familiarity, while unpredicted ones are recollected.
- Nonetheless, the neural processes underlying this difference have not been thoroughly explored.
- To conclude, a comparison of the neural correlates of PE can enhance our understanding of the conditions under which PE enhances memory performance.
- **Dissertation aim 2:** Investigating the ERPs of PE in relation to episodic memory.

1.3. Predictive Account Across the Lifespan

From childhood to old age, there are continuous changes in episodic memory processes. Existing literature indicates a pattern of rapid improvement during childhood, followed by a peak and subsequent decline during adulthood (Langnes et al., 2019; Shing et al., 2016). Moreover, this age-specific pattern of episodic memory has been linked to structural and functional brain correlates, specifically the MTL, the hippocamous, and the prefrontal cortex (PFC) (for reviews see (Cabeza et al., 2018; Ofen & Shing, 2013). The maturation of the hippocampal regions in early childhood has been associated with age-related memory improvement (Lee et al., 2014). At the other end of the lifespan, age-related impairments in MTL regions have been linked to difficulties in episodic memory processes among older adults, particularly in separating new associations from previous events (Daselaar et al., 2003, 2006). On the other hand, the PFC exhibits a more extended developmental trajectory compared to the MTL (Sowell et al., 2003). The PFC has long been associated with metamemory, which refers to the ability to monitor and control one's own memory functions (Janowsky et al., 1989; Schwartz, 1994). Research has demonstrated that both children and older adults often struggle with memory monitoring, leading to difficulties in recalling specific details associated with past events (Ghetti et al., 2010; Johnson et al., 1993; Souchay & Isingrini, 2004; Wahlheim & Zacks, 2019). Overall, investigations into the varying lifespan trajectories of the brain and memory functions have sought to understand the age-related effects on episodic memory processes. However, research on lifespan differences in predictive processing and its impact on memory remains relatively limited.

Taking a lifespan approach is crucial for understanding the interplay between PE and episodic memory. Although the predictive coding framework has been used to investigate disorders associated with abnormal prediction patterns (e.g., schizophrenia, Fletcher & Frith, 2008), little is known about how predictive processing develops in children and older adults who undergo significant changes in their internal knowledge structure and neurocognitive architecture. To qualify as a unifying framework of the brain, it is essential to examine the boundaries and adaptiveness of the predictive brain principle within the neuroarchitectures of both developing and aging brains. In sum, it was capitalized in the presented dissertation that the differences between the episodic memory processes across the lifespan provide a unique opportunity to derive specific hypotheses about potential age differences in predictive processing such as, how predictions are generated, and how PEs, in turn, shape the episodic memory.

1.3.1. Two-Component Framework of Episodic Memory

A notable framework, the two-component framework of episodic memory (Shing et al., 2008, 2010; Shing & Lindenberger, 2011) emphasizes the dynamic nature of episodic memory functioning throughout the lifespan. The model consists of two key interactive components: the associative component and the strategic component. The associative component facilitates the integration of various features of memory content into coherent representations, while the strategic component controls and regulates memory processes. According to the framework, these two components follow distinct developmental trajectories over the lifespan. Specifically, the associative component exhibits relatively faster development during childhood and undergoes a decline in late adulthood and old age. On the other hand, the strategic component matures later, but also shows a decline in older age, similar to the associative component.

There is ample evidence available on the age-related differences in the neural and behavioral correlates of the two components of episodic memory. For instance, the seminal study from Moscovitch (1992) proposed that strategic component primarily relies on the frontal cortex, whereas the associative component predominantly related to the MTL regions, specifically the hippocampus. Research has provided an empirical support for this neural and structural distinction between the associative and strategic components (Shing et al., 2008; Werkle-Bergner et al., 2006). For the associative component, studies suggest that the maturation in MTL areas during childhood is correlated with improvements in the ability to form and remember associations between different elements of an event (Daselaar et al., 2003; 2006). On the other hand, the strategic component has been linked to the PFC in the processes related to memory control (Fletcher & Henson, 2001; Rugg & Wilding, 2000). At the other end of the life span, there is a decline in activity within posterior brain areas but an increasing activity in frontal areas (Davis et al., 2008; Grady et al., 2003). This shift in older age may reflect a compensatory mechanism for difficulties in forming new associations and integrating of new information (for a review see Maillet & Rajah, 2013). Moreover, research has shown that older adults exhibit higher activation in the anterior cingulate cortex (ACC) during conflict monitoring compared to younger adults (Davis et al., 2008; Jimura & Braver, 2010), which suggests that older adults may rely more extensively on cognitive control mechanisms in the ACC to resolve conflicts. Conversely, during memory development in children, significant changes in frontal areas and their interaction with MTL are primarily associated with processes involved in organizing and structuring information for later recall (Nolden et al., 2021; Ofen et al., 2007). All in all, the differences in neural and behavioral aspects of the associative and strategic component suggest that the challenges in episodic memory for children stem mainly from underdeveloped strategic operations, while the difficulties experienced by older adults are associated with impairments in both the associative and strategic components.

The first direct evidence for the two-component framework was provided by Shing et al.'s (2010) study. In the study, the authors investigated age-related differences in the associative and strategic components within a similar task across four age groups (children, teenagers, young and older adults). Participants were required to remember words and words pairs, and the task included two manipulations: the associative component involved forming associations between the words, while the strategic component involved utilizing memory strategies to enhance memory performance. During the task, participants were given different instructions that emphasized either item encoding, pair encoding, or elaborative pair encoding as a strategy. The results were in line with the notion that distinct patterns of memory performance are observed across different age groups. Specifically, children exhibited the greatest benefit from the combined instructions, indicating their reliance on associative binding. In contrast, older adults did not show a memory benefit related to the task instructions, suggesting a decline in both the strategic and the associative components. Taken together, these findings support the different developmental trajectories of the two components of episodic memory. It suggests that children may have tendency to benefit from associative strategies to bind different features of an event, while older adults may have difficulties in employing effective strategies for processing new information.

1.3.2. Pattern Completion and Pattern Separation

Previous research has demonstrated that the ability to form and remember precise memories, characterized by specific details and without confusion with similar information, undergoes changes throughout lifespan (Graf & Ohta, 2002; Ofen & Shing, 2013; Sommer et al., 2021). This adaptive encoding, remembering, and discrimination of different memories rely on the interplay between two crucial processes: pattern completion and pattern separation (McClelland et al., 1995; Ngo et al., 2021). Pattern completion serves as a mechanism for memory retrieval by activating a network of related elements or constituents of an event. When pattern completion occurs, the activation of one element can trigger the retrieval of other associated elements within the same event. In contrast, pattern separation involves extracting unique features or details that enable the differentiation of similar events from one another. This process aids in encoding similar events as distinct, non-overlapping representations in memory, preventing them from being conflated.

Studies have indicated that children demonstrate improved ability to remember associations, aided by pattern completion processes (Ngo et al., 2018). However, their memories are also heavily influenced by specific perceptual properties rather than abstract or semantic knowledge (Ofen & Shing, 2013), suggesting a pattern separation-like process. Previous research has highlighted the involvement of the hippocampus in both pattern separation (Doxey & Kirwan; 2015; cf. Quian Quiroga, 2020) and pattern completion (Schapiro et al., 2012). Regarding the development of the hippocampal regions, it has been proposed that children's ability to form distinct memories and bind them together aligns with age-related improvements in pattern separation and completion during childhood (James et al., 2021; Ngo et al., 2018; Rollins & Cloude, 2018). Conversely, at the other end of the lifespan, older adults tend to rely more on general concepts and similarities, resulting in difficulties in discriminating similar events (Fandakova et al., 2018). Studies have consistently shown reduced neural distinctiveness in older adults when presented with different events compared to young adults (Koen et al., 2019; Park et al., 2010, 2012; Sommer et al., 2019). This loss of details may be associated with older adults' difficulties in forming new memories. Taken together, the evidence suggests that a developmental trajectory wherein the precision of encoding and retrieval improves from childhood to adulthood and then declines during aging.

1.3.3. Interim Summary

By integrating evidence from various research domains that investigate changes in memory processes across the lifespan, it becomes reasonable to assume that the differences in episodic memory processes may impact how predictions are generated and how violations to predictions affect memory. Additionally, considering the role of pattern separation in supporting subsequent memory for unexpected events (Aitken & Kok, 2022) Frank et al., 2020), the neural and behavioral changes underlaying the relationship between PE and episodic memory are expected to change over the lifespan, as well. Specifically, children may be more sensitive to events that elicit PE due to their bias towards the associative component, resulting in more pronounced PE and enhanced subsequent memory. In contrast, older adults may exhibit reduced sensitivity to the effects of PE on memory, as the associative component tends to decline with age and predictions based on previously formed associations become less reliable. However, despite the potential significance of these assumptions for the literature, there is a scarcity of empirical research examining the lifespan differences in the relationship between PE and episodic memory. Lifespan studies play a crucial role in bridging the gaps between specific age periods studied in psychology and cognitive neuroscience, enabling a comprehensive understanding of memory and prediction processing throughout the lifespan. Such comparisons provide valuable insights that would not be attainable without this broader perspective. In this dissertation, the investigation of predictive processing in different age groups provides a better understanding of the relationship between PE and episodic memory, shedding light on the dynamics of this interaction across the lifespan.

- The two-component framework of episodic memory comprises two interactive components which change over the lifespan: associative and strategic.
- The associative component develops relatively faster in childhood than the strategic component, whereas both components decline similarly in older age.
- It can be hypothesized that children are more sensitive to PE, as they are biased towards the associative component. Conversely, older adults may be less sensitive to PE, as the associative component declines with age.
- However, there is no previous research on lifespan differences in predictive processing and its effect on memory.
- It is crucial to investigate how PE affects memory processes in both developing and aging brains to fully comprehend the mechanisms of PE and episodic memory.
- **Dissertation aim 3:** Investigating age differences in the relationship between PE and episodic memory.

1.4. The Aims and the Relevance of the Presented Work

In this dissertation, we aimed to gain valuable insights into the fundamental processes related to PE that shape our cognitive experiences and contribute to our understanding of how memories are encoded, stored, and retrieved. Three main research goals were pursued to address these objectives.

Study 1 explored and addressed the limitations and gaps in previous research on the manipulation of the U-shaped function of PE on memory. By incorporating three levels of PE in one experimental setup, this study offered a comprehensive and nuanced approach to understanding the effects of PE on episodic memory. The inclusion of a medium level that was previously lacking in the literature added depth and richness to the investigation. Through two carefully designed experiments, this Study 1 provided a broader perspective on the relationship between PE and episodic memory. The objective of Study 2 was to investigate neural ERP correlates associated with encoding and retrieval of events accompanied by PE. While previous research has explored the differential processing of expected and unexpected events, no previous studies have examined the role of PE, as reflected by P3 amplitude, in subsequent memory benefits. Furthermore, the distinct neural processes involved in the retrieval of PE, specifically familiarity and recollection, have not been fully understood. By analyzing the ERP correlates associated with these processes, Study 2 aimed to provide crucial insights into the conditions under which PE enhances memory performance. Study 3 adopted a lifespan approach to investigate the interplay between PE and episodic memory processes, offering novel insights into the cognitive mechanisms underlying memory across different age groups. Little is known about how predictive processing evolves in children and older adults, who undergo substantial changes in their internal knowledge structures and neurocognitive architectures. To establish the predictive coding framework as a unifying framework of the brain, it is imperative to investigate the boundaries and adaptiveness of the predictive coding framework within both developing and aging brains. By investigating age-related differences in the relationship between PE and episodic memory, Study 3 aimed to fill these knowledge gaps related to the generation of predictions and the impact of PE on shaping episodic memory.

To conclude, this dissertation aimed to provide a broader understanding of how PE affects episodic memory. The proposed U-shape effect of PE on memory, its ERP correlates, and age-related differences in the processes of PE were investigated. Last but not least, it is worth highlighting that all three studies presented in this dissertation adhered to Open Science Practices to ensure research integrity and transparency. This included preregistration of research and analysis plans, sample size justifications, reporting deviations from the original plans and open availability of materials, data, and code in online repositories. Through these transparent research practices, unique perspectives on the effects of PE on episodic memory were offered, promoting accessibility and scientific progress.

2. Summary of Empirical Studies

2.1. Study 1 - From Generating to Violating Predictions: The Effects of Prediction Error on Episodic Memory

2.1.1. Background

The ability to generate predictions and adjust them when there is a discrepancy between the predictions and incoming sensory information (i.e., PE) is essential for adaptive behavior. Recent research has identified several factors that influence subsequent memory performance, such as the memory congruency effect and memory benefit for PE. As a result, the U-shaped relationship has been postulated, with low and high levels of PE leading to better subsequent memory performance compared to medium levels. However, previous studies (Bein et al., 2021; Greve et al., 2018; Kafkas & Montaldi, 2018) lacked a comparable medium level of PE that is related to previously induced prediction generation in episodic memory context. In our two preregistered studies, we aimed to fill this gap in the literature by investigating the impact of varying levels of PE on episodic memory.

Pre-registered hypoteses:

- There is a U-shape relationship between PE level and recognition memory: Low and high PE levels have better recognition memory performance in comparison to medium PE.
- Association memory performance varies as a function of PE: High PE level has better association memory performance than low and medium PE.
- There is a difference between confidence ratings across different PE levels: High PE levels have higher confidence ratings compared to the other levels of PE.

2.1.2. Method

Two experiments were conducted to test the U-shaped function of PE on memory. In both experiments, we followed the same overall structure: The experiments were conducted over two consecutive days, with the prediction learning phase on the first day and the encoding of PE and surprise memory test phases on the second day. Initially, we asked the participants to learn associations between cue-target pairs, to let them generate predictions based on these associations. Based on the studies on statistical learning (Kim et al., 2017; Schapiro et al., 2012; Turk- Browne et al., 2012), participants develop the ability to predict targets after repeated exposure and learn the associations between cue-target pairs. Subsequently, we violated their predictions with individual items in three PE levels: low, medium, and high. Finally, we evaluated subsequent memory performance for the individual items and their associations.

The two experiments differed in several key aspects. (i) In Experiment 1, the PE levels were generated based on semantic sub-categorization (i.e., instrument sounds and object categories, please see below for details). However, to rule out potential effects of semantic knowledge, in Experiment 2, the associations between artificial creatures called “Wubbels” and their environments were used. (ii) In Experiment 1, the contingency structure was built during the prediction learning phase. This might have affected participants’ sensitivity to medium and high PE trials during the encoding phase. To address this, Experiment 2 had a deterministic prediction learning phase where the contingency between cue and targets was set to 100 %. (iii) in Experiment 2, two additional aspects of associative memory were measured namely Wubbel-scene and Wubbel-location pairs to provide a more comprehensive assessment of associative memory compared to Experiment 1.

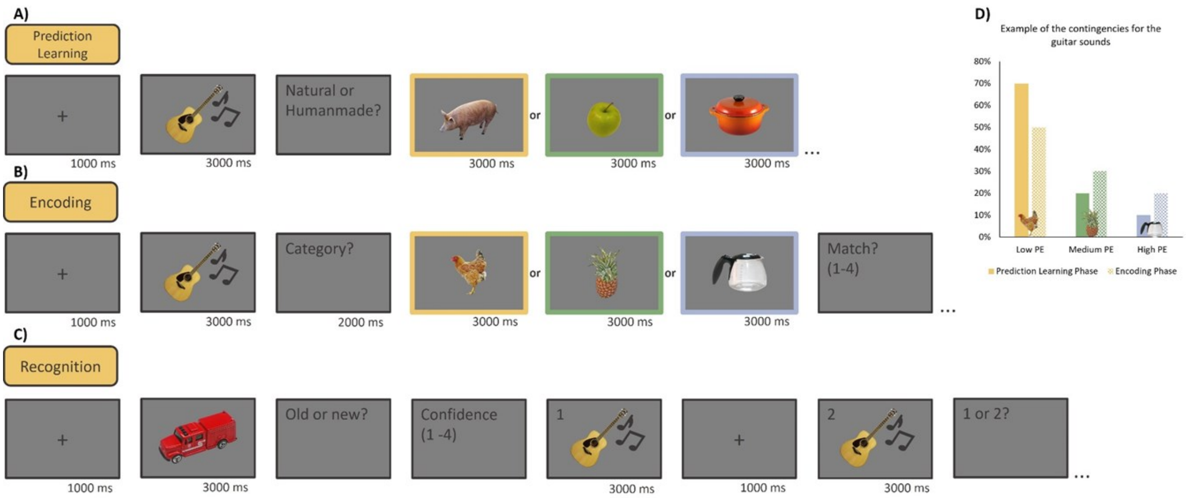
2.1.2.1. Experiment 1. In Experiment 1, 60 university students participated in the study (46 females and 14 males, aged 18–29 years, mean age = 21.92 (SD = 2.84)). Musical instrument sounds and object pictures were used as stimuli. Four categories of musical instrument sounds, namely guitar, trumpet, violin, and piano, each with eight distinct sounds, were selected. The object pictures were evenly divided into two main categories, natural and human-made, each with two sub-categories. The natural objects were classified as animals and fruits/vegetables/nuts, while the human-made objects were categorized as household and toys/school/sports objects.

The study structure for Experiment 1 can be seen in Figure 1. The study was conducted over two consecutive days and consisted of three phases: prediction learning, encoding, and recognition. On the first day, during the prediction learning phase, participants were presented with musical instrument sounds and asked to predict whether the upcoming object would be natural or human-made. After participants’ response, an object exemplar was shown. The contingency structure for the associations between sounds and object categories was derived from one of the main categories, namely natural or human-made, with varying degrees (i.e., low, medium, and high). The contingency structure for the encoding phase was 70% (low PE), 20% (medium PE), and 10% (high PE). For example, as shown in Figure 1, if guitar sounds were associated with animal exemplars, for later, presenting an animal object would elicit a low level of PE, a fruit object would elicit a medium and a human-made object would elicit a high level of PE.

The second day started with the encoding phase where participants were presented with sounds and predicted the most likely object category among four different sub-categories. They were then shown novel object pictures and indicated if the presented object belonged to the predicted category. The contingency structure for the encoding phase was 50%, 30%, and 20% for low, medium, and high PE levels, respectively, to maintain the original contingencies as close as possible to the prediction learning phase while increasing the number of trials possible for the weakly associated category. After the encoding phase, the recognition phase was studied where participants were asked to make old/new judgments on the test pictures with their confidence ratings. For the associative memory phase, participants were asked to indicate the paired sound as well.

Figure 1

Study Design for Experiment 1



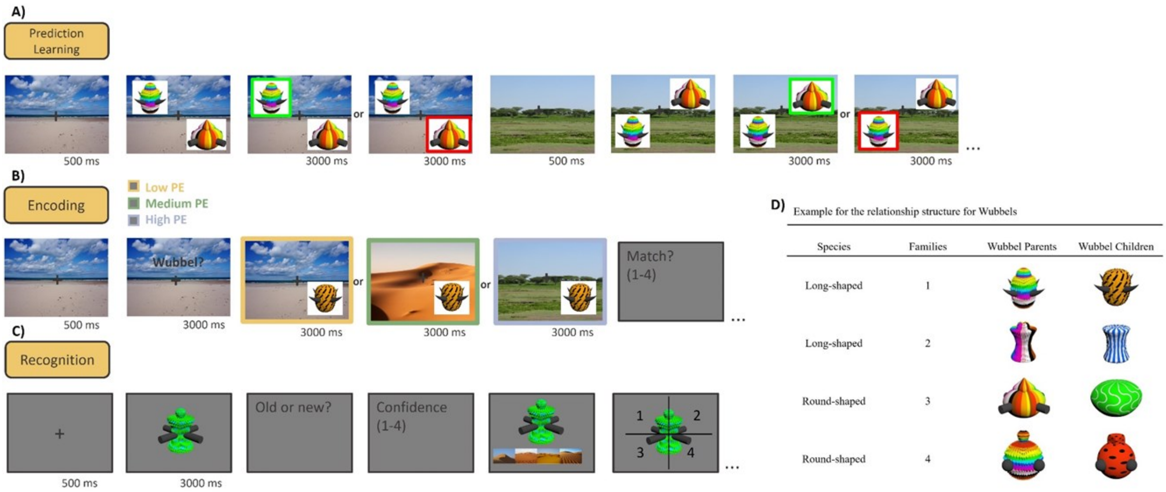
Note. A. On Day 1, participants were asked to make predictions about sound-object category associations. During the prediction learning phase, participants were presented with a musical instrument sound and asked to predict the upcoming object category based on two levels. After their response, an object exemplar was shown. As in the example in Panel D, the guitar sounds were followed by exemplar objects from animal categories 70% of the time (Low PE, yellow). Thus, the contingencies for exemplar objects from fruit categories (Medium PE, green) and human-made categories (High PE, blue) were 20% and 10%, respectively. B. On Day 2, for the encoding phase, a sound was presented, and participants were asked to predict the most likely object category among four different sub-categories. Participants were then presented with object pictures and asked to indicate if the presented object belonged to the same category they predicted. The contingency structure was 50%, 30%, and 20% for low, medium, and high PE levels, respectively. C. During the recognition phase, participants were asked to make old/new judgments on the test pictures with their confidence ratings, and they were asked to indicate the paired sound as well. D. An example of the contingency structure for the guitar sound.

2.1.2.2. Experiment 2. In Experiment 2, 51 participants (28 females and 23 males, aged 18-35 years, mean age = 23.14 (SD = 4.49)) were recruited. As study material, we used artificial creatures called "Wubbels" and natural environment pictures to prevent the influence of prior knowledge. Four distinct categories of environments (i.e., beach, snowy mountains, desert, and savanna) were selected. The Wubbels were structured into two main groups: the Wubbel parents used in the prediction learning phase and the Wubbel children used in the encoding and recognition phases (see Figure 2D). The body shapes of the four Wubbel families were consistent with their primary species, and each prototype had a unique combination of features complementing its body. The parents differed in the assigned color patterns, while the children had varying features, such as hat shape, arm shape, skin type, body color, pattern color, and pattern. The purpose of these design variations was to maintain similarity among the children based on key features shared with the parents and to establish relationships between certain families of Wubbels.

Figure 2 shows the study structure for Experiment 2 which involved three phases: prediction learning, encoding, and recognition. In the prediction learning phase, participants learned associations between Wubbel families and environmental categories. Participants were presented with two Wubbel parents from different families on different screen locations and asked to indicate which Wubbel matched the presented scene. Feedback was given based on their response. As in the example Figure 2D., participants were expected to learn that one of the long-shaped Wubbel families lives on the beach. The associations between Wubbels and environments were predetermined, and the contingency was 100 %.

Figure 2

The Study Design for Experiment 2

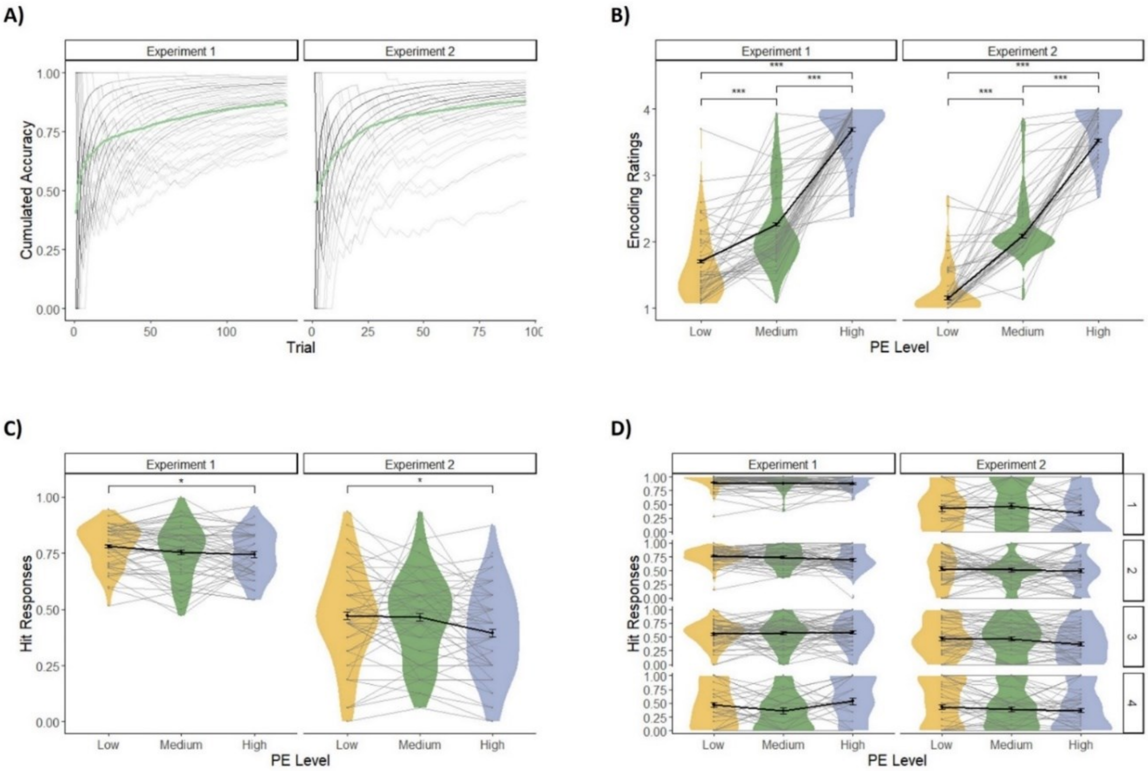


Note. A. On day 1, participants were asked to learn associations between Wubbel families and environment categories. In each trial of the prediction learning phase, participants were presented with two Wubbel parents from different families on different screen locations and asked to indicate which Wubbel matches the presented scene. Participants received feedback based on their response. For example, participants were expected to learn that one of the long-shaped Wubbel families lives on the beach. B. On day 2, the encoding phase was conducted first. Participants were presented with a scene and asked to predict the most likely Wubbel family in their minds. Then, a Wubbel child was presented on one of four possible screen locations. Participants were asked to indicate whether the presented Wubbel child belongs to the family which they predicted. For example, a long-shaped Wubbel child presented in a beach scene would elicit a low PE (yellow). Presenting the same Wubbel in a desert, which was an environment for the other long-shaped family, would lead to a medium PE (green). Lastly, presenting the same Wubbel with environments associated with the round-shaped families would elicit a high PE (blue). C. During the recognition phase, participants were asked to make old/new judgments and report their confidence. Participants were then asked to indicate the paired scene and paired location. D. The relationship structure between Wubbel families and children is illustrated in the example.

On Day 2, the encoding phase was conducted where participants were presented with a scene and asked to predict the most likely Wubbel family in their minds. Then, a Wubbel child was presented on one of four possible screen locations. Participants were asked to indicate if the presented Wubbel child belongs to the family which they predicted. For example, a long-shaped Wubbel child presented in a beach scene would elicit a low PE, depicted in yellow. Presenting the same long-shaped Wubbel child in a desert, which was an environment for the other long-shaped family, would lead to medium PE (green). Lastly, presenting the same Wubbel child with environments associated with the round-shaped families would elicit high PE (blue). In the recall alternatives and participants had to indicate if they had seen the presented Wubbel before and rate their confidence, choose the correct scene from four alternatives, and identify the location on the screen the Wubbel was presented.

Figure 3

Results for Experiment 1 and 2



Note. A. Cumulated accuracy for prediction learning. Grey lines indicate the performance of single participants. Green lines indicate the group mean. B. Encoding ratings for low, medium, and high PE levels. C. Hit responses for low, medium, and high PE levels. D. Hit responses for low, medium, and high PE levels separated by confidence ratings (1- Very sure, 2- Sure, 3- Unsure, 4- Very Unsure). Grey lines indicate the performance of single participants. Black lines indicate the group mean with error bars reflecting ± SEM. Asterisks denote statistically significant differences, * $p < .05$, *** $p < .001$.

2.1.3. Results and Discussion

We first checked if participants generate predictions about the cue-target pairs via accuracy rates from the prediction learning phases. For both Experiment 1 and 2, accuracy rates of predicting the upcoming object category increased with trials and it was significantly different than chance levels of performance (Figure 3A). We then tested our manipulation on the PE levels. We examined the ratings for category judgment collected during the encoding phase, with the highest rating (4- Strongly no) meaning the presented object does not belong to the same category that participant predicted earlier and the lowest rating indicating the presented object belongs to the same category that participant predicted earlier (1- Strongly yes). The results showed that the three PE levels were significantly different from each other, while high PE level had the highest category judgment ratings (Figure 3B). We concluded that this result verifies our manipulation of the PE levels, such that participants reported that objects from high and medium PE levels are not from the category they predicted. Importantly, the results for the main research question on the U-shape effect of PE on memory indicated that recognition memory performance was better for low PE level than high PE level (Figure 3C). The results for association memory and confidence-weighted hit rates (Figure 3D) did not show a significant difference on the main effect of PE levels. Taken together, our results suggested a memory congruency effect and an absence of memory benefit for PE.

2.1.4. Conclusion

Study 1 provided novel paradigms to generate and violate PEs to varying degrees. The results indicate that our participants successfully learned from the provided regularities and formed predictions. While our findings provided strong evidence for the manipulation of PE, we did not observe a memory advantage for high PE levels in either the recognition or association memory tasks. Instead, we consistently found a memory advantage for low PE trials, and this is consistent with the memory congruency effect observed in previous studies (Alba & Hasher, 1983; Anderson, 1981; Craik & Tulving, 1975). We therefore conclude that the effect of PE on memory benefit is not straightforward, and there may be additional factors, such as task sensitivity concerning how PEs are experimentally generated and how their subsequent memory tested that influence its role in facilitating improved memory. Specifically, regarding the generation of PEs, previous studies reported better memory for PE had their PE manipulation on item level (Bein et al., 2021; Kim et al., 2017), whereas our manipulation was based on category level due to the nature of the tasks. In terms of retrieval of events with PE, it can be concluded that studies that found memory enhancement for PEs tested memory performance via alternative forced-choice (Greve et al., 2017; Quent et al, 2022) and mixed lists with similar lures (Bein et al., 2021; Frank et al., 2020), unlike our paradigms which used an old/new task. Thus, it is reasonable to argue that only a level of familiarity can be sufficient to dissociate the old items from the new ones, and not boost memory for high PE trials specifically. Further investigation of these modulating factors could provide valuable insights and a clearer direction for understanding the relationship between PE and memory processes.

2.2. Study 2 - Unexpected Twists: Electrophysiological Correlates of Encoding and Retrieval of Events eliciting Prediction Error

2.2.1. Background

Previous EEG research has shown that the brain processes expected and unexpected events differently, as indicated by the P3 amplitude. However, no previous studies have examined whether the process of PE reflected by P3 amplitude plays a role in remembering those events later. On the other hand, in the retrieval of PE, two distinct neural processes, familiarity and recollection, are involved. Predicted events tend to enhance familiarity, while unpredicted events are more likely to be recollected. Nevertheless, the specific ERP correlates that are associated with these differences have not been fully understood. Comparing the neural correlates of PE can provide valuable insights into the conditions under which PE enhances memory performance.

Pre-registered hypoteses:

- Better memory performance is observed for events that elicit PE compared to events that do not violate predictions.
- Violation events that are later remembered elicit higher P3 amplitudes compared to violation events that are later forgotten.
- The recollection effect is observed in ERPs for violation trials that are later remembered than later forgotten.
- The familiarity effect is observed in ERPs for non-violation trials that are later remembered than later forgotten.

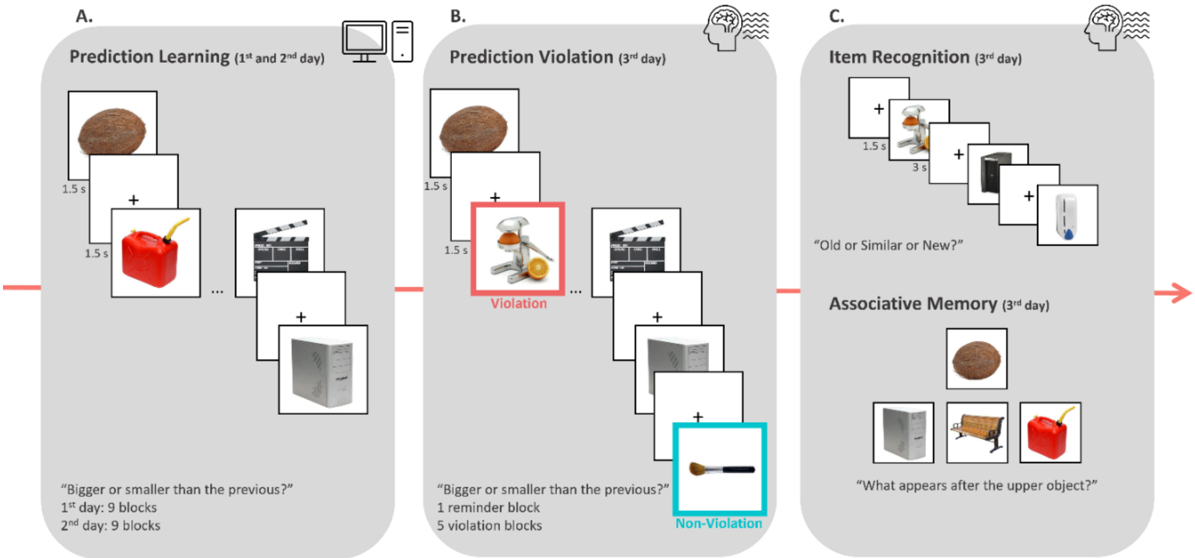
2.2.2. Method

45 university students participated in the study (32 women, 13 men, aged 18-30 years, mean age = 23.52 (*SD* = 2.67)). The pictures of everyday objects from the previous study by Bein et al., 2021 were used. The study was conducted over three consecutive days, with EEG recorded during the last day (Figure 4). On the first two days, in a statistical learning paradigm, participants implicitly learned sequentially presented object pairs embedded within a stream of objects (i.e., prediction learning phase). Participants were presented with object pictures and asked to indicate if the presented object was bigger or smaller than the previous one. Unbeknownst to the participants, the task was structured in such a way that there were pairs of

objects that always followed each other. On the third day, new objects which had not been presented before (i.e., violation phase) were added. Half of the objects were inserted instead of the second item of the pair, eliciting PE (violation items). The other half of the objects were presented between pairs to create a base line (non-violation items). Hereafter, item recognition memory was tested for violation and non-violation items via old, similar, and new task. Lastly, associative memory was assessed for the original pairs that were studied during the prediction learning phase. This method allows us to have an item level PE manipulation and more sensitive measure for memory performance via similar lures.

Figure 4

Study Design



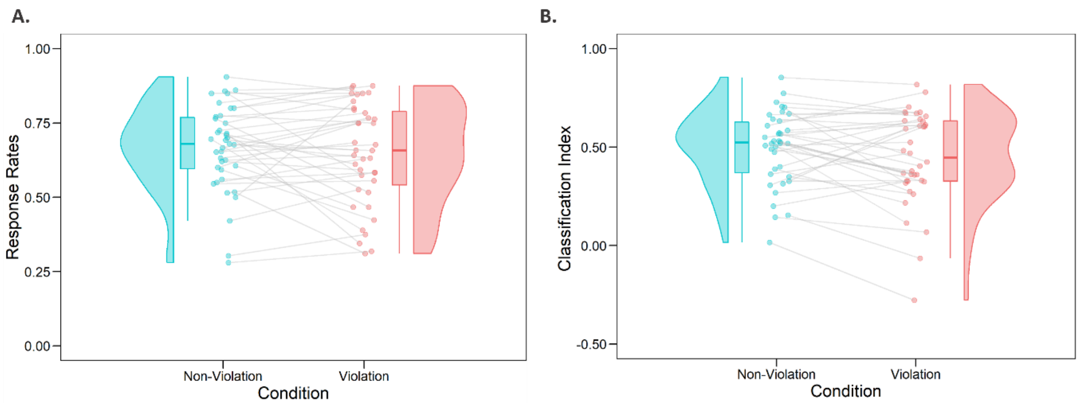
Note. A. During prediction learning (Day 1 and 2), participants viewed pairs of sequentially presented objects and asked to indicate whether each object was bigger or smaller than the previous object. B. In the prediction violation phase (Day 3), new object pictures were inserted into the sequence of objects, either instead of the second object in the pair (violation) or after the second object in a pair (non-violation). C. Following the violation phase, participants completed an item recognition memory test (Day 3) where they were presented with violation and non-violation, similar lures, or new items, and asked to indicate whether each item was old, similar, or new. Memory for the original predictive pair was also tested (Day 3) by presenting participants with the first object in a pair and asking which of three objects followed the top object.

For the behavioral measures to test the effect of PE on memory, we calculated two main measures: response rates and a classification index. Response rates were computed as "old" response rates to violation and non-violation items and the classification index was assessed to capture mnemonic discrimination via precision and sensitivity measures. Precision was computed as the ratio of correct old responses to old items, whereas sensitivity was calculated as the proportion of correctly identified trials out of total. Then, classification index was calculated by multiplying precision and sensitivity by two, adding them together, and lastly dividing by the sum of precision and sensitivity (Ngo et al., 2020).

For the neural correlates of PE, we used ERPs that were time-locked to the onset of stimuli. P3 mean amplitude values were measured during the prediction learning phase. The mean amplitude values of familiarity and recollection components were measured during the recognition phase. We decided on the time windows and topographical positions for our components by means of the previous literature (Polich, 2007) and our pilot study. Also, the validity of time windows was checked with cluster-based permutation tests. The P3 was obtained from 400 – 800 ms at centroparietal electrodes. The familiarity component was obtained from 300 – 500 ms at frontocentral electrodes. The recollection component was obtained from 400 to 800 ms at parietooccipital electrodes.

Figure 5

Response Rates and Classification Index



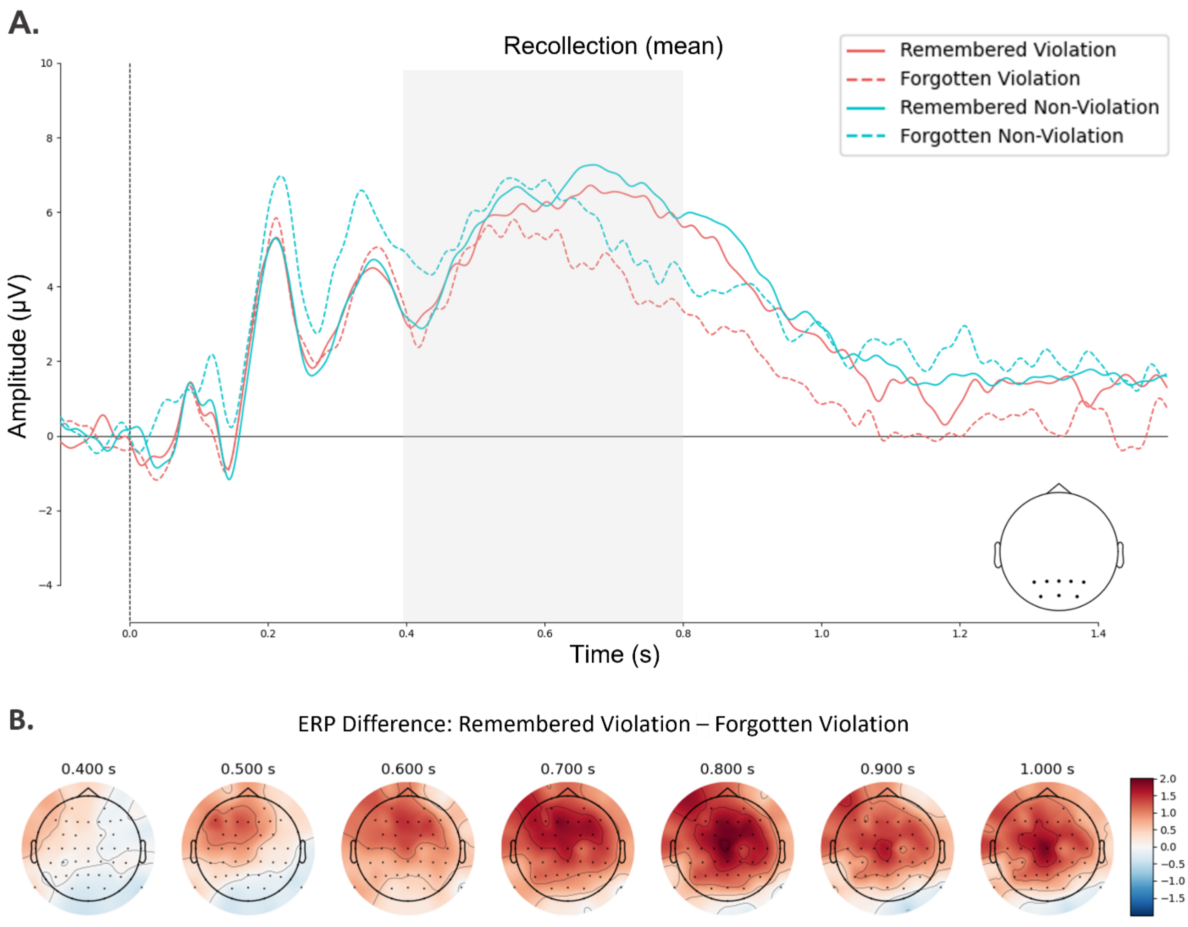
Note. The raincloud plot shows the distribution of response rates and classification index for violation and non-violation conditions. A. Proportion of old responses to old items. B. The proportion of correct responses (true positives and true negatives) out of all instances. The box plots display the median, interquartile range, and 95 % confidence interval for each group using, while the density plots show the distribution of the data points for each condition. The individual data points are displayed as scatter plots.

2.2.3. Results and Discussion

Since the primary objective of the study was to examine the effects of PE on memory, we first checked if participants learned the object pairs to build up predictions to ensure clear interpretation of the results. With this aim we analyzed reaction times (RTs) during the prediction learning phase and accuracy rates during the associative memory phase. The results indicated that participants were faster for the second item of the pair compared to the first item, suggesting a learning process due to prediction of the upcoming object. Participants selected associated pairs significantly above the chance level, again indicating a successful learning process. For the main research question, the results for the effects of PE on memory were not significantly different between violation and non-violation items neither for response rates nor for classification index (Figure 5). Although we did not find a behavioral effect, we proceeded to investigate the neural correlates of PE, as they could give better insights into mechanisms involved in encoding and retrieval processes of PE.

Figure 6

Recollection component during the item recognition phase

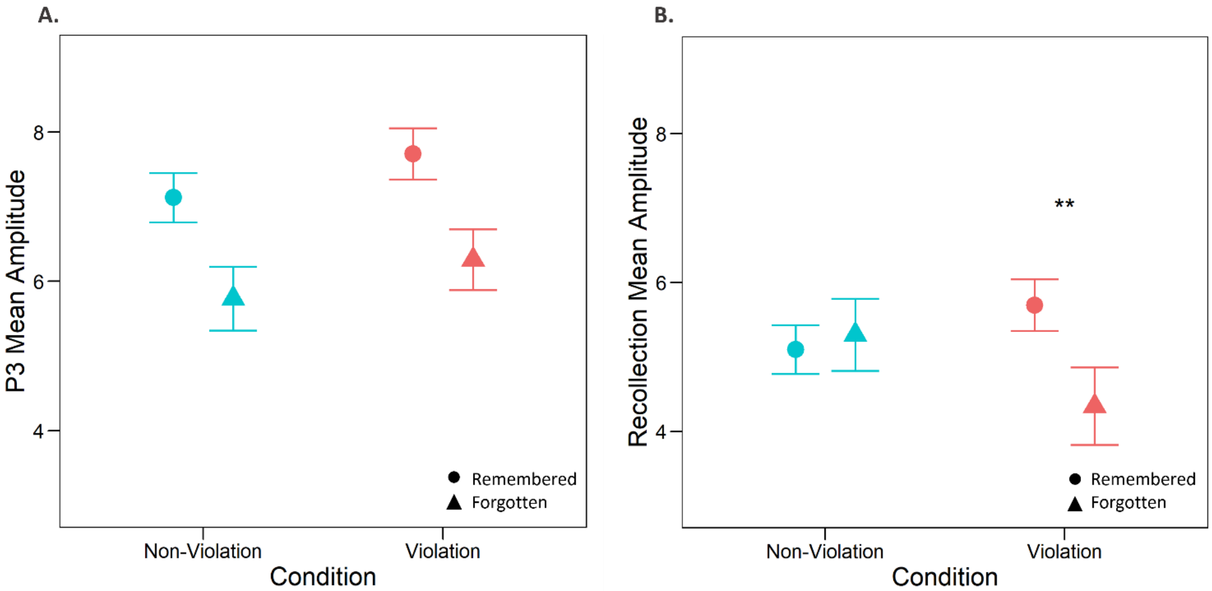


Note. Stimulus-locked ERPs during the item recognition phase. A. Color-coded ERP grand average recorded at parietooccipital electrodes with highlighted time window in gray. B. Topographical map plot of remembered violation minus forgotten violation difference in the recollection component time window.

We observed a significant relationship between the recollection component and item recognition memory for previously violated items (Figure 6 and 7). Our results revealed that there was an interaction effect, indicating higher amplitude values were obtained for remembered violation items compared to forgotten violation trials, while no difference was observed between remembered and forgotten non-violation items. The results for the familiarity component did not show a significant effect of PE. Additionally, we did not find a relationship between P3 mean amplitude during encoding, PE, and subsequent memory (Figure 7). Overall, these findings suggest that recollection plays an important role in the interplay between PE and episodic memory. Furthermore, our exploratory analysis confirmed that the pre-registered time windows for ERP components aligned with the cluster-permutation results, validating our approach in selecting relevant time-windows of interest.

Figure 7

Average ERP amplitude values



Note. Average ERP amplitude values for each condition within the relevant time windows. Error bars represent the within-participant standard error of the mean. A. Mean amplitude values of P3 component during the violation phase. B. Mean amplitude values of recollection component during the item recognition phase. ** $p < .01$.

2.2.4. Conclusion

Study 2 investigated the ERP correlates of PE during encoding and retrieval within the same paradigm. Contrary to our expectations and the results from previous research (Bein et al., 2021), no memory advantage was found for items generating PE. However, this study highlights the significance of recollection in understanding how PE influences episodic memory. These findings suggest that violation of expectations enhances recollection, aligning with previous research on the retrieval-enhancing effects of PE (Kafkas & Montaldi, 2018) and the role of memory-guided predictions in enhancing recollection (Fenerci & Sheldon, 2022; Henson & Gagnepain, 2010; Theobald et al., 2022; Van Kesteren et al., 2012; Wahlheim et al., 2022). Our results emphasize that deviations from expectations generate a stronger recollection signal, potentially facilitating better subsequent memory. Overall, our study contributes to the growing knowledge of the complex nature of PE and its relationship with memory processes. We provide insights into the underlying neural mechanisms involved. However, further research is warranted to identify a reliable condition or understand the moderator effects that determine how PE enhances subsequent memory.

2.3. Study 3 - The impact of mnemonic prediction errors on episodic memory: A lifespan study

2.3.1. Background

The two-component framework of episodic memory encompasses two interactive components, namely the associative and strategic components, which undergo changes throughout the lifespan. The associative component exhibits relatively faster development during childhood compared to the strategic component, while both components demonstrate similar declines in older age. Given these developmental trajectories, it can be hypothesized that children, with their reliance on the associative component, may be more sensitive to PE compared to older adults, whose associative component diminishes with age. However, there is a lack of previous research investigating lifespan differences in predictive processing and its impact on memory. Therefore, it is crucial to examine how PE influences memory processes in both developing and aging brains to gain a comprehensive understanding of the mechanisms underlying PE and its relationship with episodic memory.

Pre-registered hypoteses:

- Memory performance for items that violate predictions are expected to be better than those for items that do not violate a prediction.
- The expected difference in memory performance is the greatest in children, followed by young adults, and the smallest in older adults.
- No differences are expected in “old” responses for similar lures.

2.3.3. Method

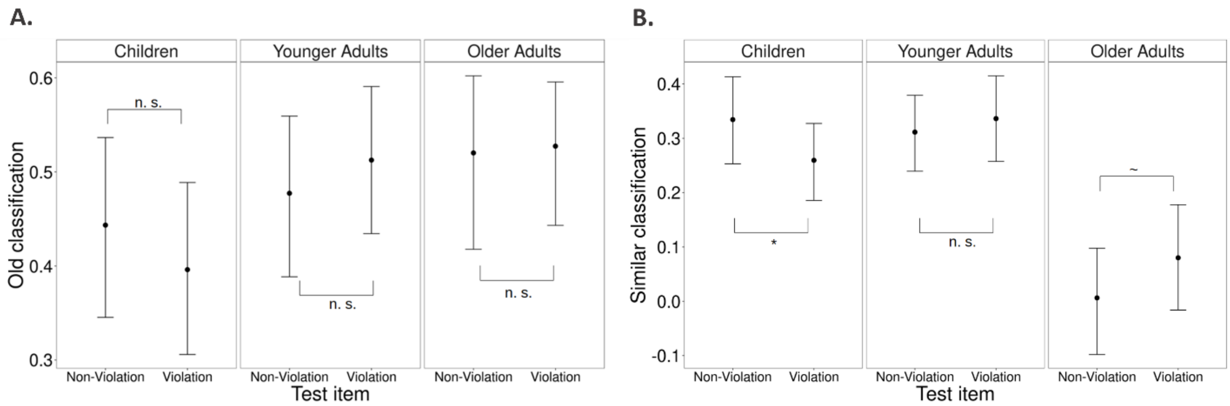
We tested 85 children (10-12 years old), 48 younger adults (18-30 years old), and 50 older adults (66-70 years old). The age ranges for children were chosen based on the understanding that the development of MTL-based associative binding undergoes significant changes during this developmental period. We can observe the enduring influence of PE during pre-puberty stages. As for older adults, their MTL structural and functional integrity is likely to decline by this age, although semantic memory functioning remains relatively intact until around 70 years of age, before the retirement period. Despite the procedural differences due to online testing, the identical statistical learning paradigm as in Study 2 was employed (Figure 4). Briefly, participants learned pairs of objects over two days and their memory was tested on the third day. The test included new objects presented either after the first item of a pair (i.e., violation items) or between pairs (i.e., non-violation items). As in Study 2, response rates and classification indices (Ngo et al., 2020) were calculated.

2.3.4. Results and Discussion

The results from response rates showed that there was no memory enhancement effect of PE in any of the age groups. The findings regarding the classification indices (Figure 8) showed no significant effects on classification for old items. However, for similar items, a significant main effect of age group was found. Contrary to the hypothesis, children showed better classification for non-violating similar items compared to violating similar items.

Figure 8

Classification results for old and similar items



Note. Error bars depict confidence intervals A. Classification of old items. B. Classification of similar items. * $p < .05$, ~ $p < .10$, n.s. non-significant

2.3.5. Conclusion

The aim of our study was to comprehensively investigate the influence of prediction PE on episodic memory across different age groups. As in Study 1 and 2, our results did not yield memory enhancement effect of PE in any of the age groups. This suggests that the role of PE in modulating episodic memory may not be as strong or consistent as previously assumed. Interestingly, our study revealed novel findings regarding the memory performance of children. We observed that non-violation items were remembered in greater detail compared to violating items. This memory advantage for non-violating items in children represents a new and intriguing finding, which warrants replication and further investigation in future research. In summary, our study challenges the notion of PE as a robust facilitator of episodic memory across the lifespan. Our results emphasize the need for careful consideration and rigorous investigation of the factors influencing the relationship between PE and memory. Moreover, the observed memory advantages for non-violation similar items in children highlight the importance of exploring additional factors that may influence memory processes.

3. General Discussion

The aim of the presented dissertation was to investigate the impact of PE on episodic memory. In Study 1, participants were trained on cue-target category associations and later exposed to violations of associations with varying levels of PE. The results showed no memory advantage effect of PE on recognition and associative memory but revealed a memory congruency effect. In Study 2, we used object pairs and violated predictions at the item level. The behavioral findings aligned with Study 1, indicating a lack of the boosting effect of PE on memory. However, the analyses of ERPs highlight the significance of recollection in the relationship between PE and memory. In Study 3, participants from different age groups, children, young and older adults, underwent the same paradigm as in Study 2. Again, the results indicated the absence of memory-enhancing effect of PE. Nevertheless, age comparisons offered insights into the developmental aspects of memory specificity. In conclusion, our consistent findings underscore the complexity of the effects of PE on episodic memory, suggesting the presence of other modulating factors that warrant further investigation.

3.1. PE Does not Generally Enhance Memory

None of the three studies revealed a subsequent memory advantage for events that violate predictions. This consistent finding suggests that the impact of PE on memory is not as straightforward and consistent as previously demonstrated. Relatedly, our findings align with a recent study by Ortiz-Tudela et al. (2023) that also reported no memory improvement for PE using continuous manipulation. It is worth noting that, in our studies, the results from the encoding phases demonstrated that the task structures effectively generated violations for the previously learned associations. We examined response ratings (Study 1), the P3 component (Study 2), and RT savings (Study 1 & 2) as indicators of our experimental manipulations on PE. Our results confirmed that PE trials indeed violated predictions. However, this effect did not translate into improved memory performance. Thus, it can be concluded that while PE is commonly assumed to drive new learning (Greve et al., 2017), its direct impact on memory may depend on various factors that require careful consideration. In the following, the methodological differences to other studies and the possible moderating factors that might influence the relationship between PE and episodic memory will be discussed.

3.1.1. Methodological considerations

One possible explanation for the absence of a memory benefit for PE in our studies could be attributed to the task sensitivity in terms of how PEs were experimentally generated and tested. It is important to consider the operational structure of the encoding and retrieval processes. Previous studies that reported memory benefits for PE often manipulated and tested PEs at the item level (Bein et al., 2021; Kim et al., 2017). In Study 1, due to the nature of our task, our manipulation was conducted at the categorical level to generate a medium level of PE that was related to previous learning. Consequently, the findings from Study 1 could be attributed to the differences between the item-level and categorical-level task structures. It is possible to assume that our participants primarily focused on the category-level information during encoding rather than on individual items that were tested later. However, in Studies 2 and 3, where the task structure was at the item level, we still did not observe the beneficial effect of PE on memory. Moreover, the evidence from studies which used category level manipulation of violation, reported a memory enhancement for the events that deviate from the previously expected ones (Frank et al., 2020; Kafkas, 2021; Kafkas & Montaldi, 2018). Thus, we can conclude that the categorical level manipulation of violation should not be a main concern and that there must be other factors influencing the nuanced relationship between PE and memory.

Following the experimental differences that might play a role on the relationship between PE and subsequent memory, it is plausible to speculate that the methods used to assess memory performance might have influenced our results. Previous studies that demonstrated a memory-enhancing effect of PE utilized memory tests such as alternative forced-choice tests (e.g., Greve et al., 2017; Quent et al., 2022) or mixed lists with similar lures (e.g., Bein et al., 2021; Frank et al., 2020), whereas Study 1 employed an old/new paradigm. It can be argued that PE facilitates memory through a pattern separation-like process by creating distinct memory snapshots. Therefore, to effectively track memory traces and rule out familiarity effects, the effect of PE on memory should be assessed with more sensitive measures. In Study 1, we addressed the familiarity issue by assessing memory performance through confidence ratings. However, even with confidence-weighted hit rates, the results did not indicate a memory benefit for high PE. Furthermore, in Study 2 and 3, despite incorporating a recognition phase with similar lures and employing more sensitive measures than old/new tasks (i.e., classification indices), the results did not yield an effect of PE on subsequent memory. Considering the other studies that used the same task structure (Bein et al., 2021) reported an effect, it is unlikely that task sensitivity alone can explain our results. Therefore, we will explore other potential moderating factors that may elucidate our findings.

3.1.2. Possible Moderating Effects between PE and Subsequent Memory

Once we rule out the potential effects of task sensitivity in generating and testing PE, we can further explore other factors that may contribute to the relationship between PE and memory. These factors include the strength and precision of prior expectations (Greve et al., 2018; Ortiz-Tudela et al., 2023), the novelty of the violation (Schomaker & Meeter, 2018), and the assessment of the violation (Gruber & Ranganath, 2019).

Although Study 2 and 3 followed a similar protocol to a previous study (Bein et al., 2021), there was one notable difference: the extended prediction generation phase. In order to ensure an effective learning threshold for the EEG signal in Study 2 and due to the online nature of Study 3 with participants from children to older adults, we increased the number of sessions. As a result, our extended learning phase likely led to stronger predictions compared to the previous study, as evidenced by higher accuracy rates[5]. Our task involved extensive exposure to the paired structure of object associations, which may have created context surprise (Quent et al., 2021) when participants encountered non-violation items that violated the expected task structure. In other words, violation items violated the expected object at the item level, while non-violation items violated the expected task structure by presenting an object that had not been seen in that specific position before (i.e., after the second object of a pair), creating a context surprise and novelty. This distinction may have elicited different cognitive and neural responses compared to the violation items that violated the expected object at the item level. Therefore, the absence of a memory benefit for PE in our studies could be attributed to the notion that our both experimental conditions, violation and non-violation trials, were generating expectations and lead to subsequent violations of those expectations either item or context level (Schomaker & Meeter, 2018).

Regarding our results, an alternative framework can provide an explanation for the nuanced relationship between PE and memory (i.e., Prediction, Appraisal, Curiosity, and Exploration (PACE), Gruber & Ranganath, 2019). The PACE framework posits that the memory enhancement associated with PEs is not solely determined by the strength of the prediction but also by the assessment or appraisal of the PE. According to this framework, when

[5] We reported .78 and .65 accuracy rates in Study 2 and 3, respectively, compared to .60 in Bein et al., 2021.

individuals encounter a PE, it triggers an appraisal process that influences their subsequent actions and subjective experience in resolving the uncertainty caused by the PE. The assessment of a PE involves evaluating its significance and potential relevance for future functioning. If the appraisal process deems the PE as valuable and informative, it can trigger curiosity and motivation to engage with the unexpected event, leading to enhanced memory encoding. On the other hand, if the appraisal process categorizes PE as unimportant or potentially negative, it may elicit behavioral inhibition and a tendency to disregard the unexpected event, resulting in reduced subsequent memory.

In Study 1, one possible explanation is that high PE items were disregarded because the task emphasized making "better" predictions to respond accurately to the presented stimuli. During the encoding phase, participants were instructed to predict the upcoming object category, and objects with varying levels of PE were presented. To make accurate predictions for future stimuli, participants may have tended to ignore items that did not align with their predictions. This type of semantic encoding has been suggested to have adaptive value for enhancing memory system functionality, even though it may introduce distortions (Schacter et al., 2011). This focus on making better predictions and the potential lack of appraisal for the high PE trials might have resulted in reduced memory encoding for these items, and consequently lower memory performance.

Furthermore, in Studies 2 and 3, despite having a task structure that allowed for violation detection at the item level (Bein et al., 2021), the extended learning phase and stronger predictions (Quent et al., 2021) might have influenced the assessment of uncertainty resolution, as stated in the PACE framework. Participants may have exhibited a tendency to disregard the violation and non-violation items presented during the violation phase, relying more heavily on previously learned object pairs. This suggests a negative assessment of uncertainty resolution, which may reflect a tendency to have difficulties in dealing with ambiguity, potentially leading to reduced memory encoding for the unexpected stimuli. Therefore, the lack of memory benefits for PE in our studies may be attributed to participants' tendency to prioritize previously generated predictions and a negative assessment of uncertainty resolution.

To conclude, the results from the presented dissertation indicated that the impact of PE on memory may not be as straightforward as initially proposed. A methodological advantage of our study was the careful control of various factors that can influence memory such as surprise and response consistency (Antony et al., 2021; Frank & Kafkas, 2021). However, even with these meticulous controls, it is possible that the effect of PE on memory may be relatively small and not consistently observed across all studies.

3.2. Recollection Plays a Role in the Interplay between PE and Subsequent Memory

In Study 2, we observed that the recollection component amplitude was higher for violation trials that were remembered compared to those that were forgotten. Importantly, we found a significant interaction effect, revealing a substantial difference in mean amplitudes of the recollection component between remembered and forgotten violation items, but not within the non-violation items. This result suggests that the violation of expectations can enhance recollection.

Our observation of the recollection component aligns with the growing body of evidence supporting the idea that unpredicted events enhance recollection (Frank et al., 2020; Kafkas, 2021; Kafkas & Montaldi, 2018). Relatedly, previous research showed that memory-guided predictions can enhance memory performance (Fenerci & Sheldon, 2022; Henson & Gagnepain, 2010; Theobald et al., 2022; Van Kesteren et al., 2012). Memory-guided predictions refer to the process by which retrieved memories of past events influence and shape predictions during the comprehension of events. For example, Wahlheim et al. (2022) conducted a study investigating the effects of predictive-looking errors on remembering event changes. They found that memory guidance led to predictive-looking errors, which were associated with better recollection memory for changed event features. This suggests that retrieving recent event features can guide predictions during unfolding events, and PE can contribute to enhanced recollection when it is driven by expectations. Consistent with these findings, our study revealed a recollection effect specifically for violation items, which were presented as replacements for the second object of the pairs that participants had predicted to see. This indicates that deviations from expected events generate a stronger recollection signal, potentially facilitating better subsequent memory.

In summary, our findings highlight the importance of recollection in the mechanisms underlying the interplay between PE and episodic memory processes. It contributes to the growing understanding of memory-guided PEs and their impact on subsequent memory performance.

3.3. Children were Better to Remember Details of Non-Violation Items

In Study 3, we found that children exhibited more specific memory for non-violation items compared to violation items. This means that children were better at recognizing similar lures and less likely to confuse them with old items when the items did not violate the expected structure. It suggests that children showed increased pattern separation for non-violation items compared to violation items. Previous research has indicated that in young adults, PE leads to the encoding of distinct memory traces, where events associated with PE are remembered separately from previous memory traces (Aitken & Kok, 2022; Frank et al., 2020). This clear separation of memory traces helps avoid interference and allows old and new memory traces to coexist without competing. However, in our study with children, an opposite pattern was observed.

An explanation for our finding can be attributed to the effect of context surprise (Quent et al., 2021). As previously stated, due to the online procedure of the task, we extended the prediction learning phase, which may have increased context surprises for non-violation items. Briefly, non-violation items might violate the task structure by being presented as singletons, not as part of previously learned paired structure. As children tend to have a bias toward the associative memory component (Shing et al., 2008, 2010; Shing & Lindenberger, 2011), they may have formed stronger associations with the task structure and processed non-violation items more deeply compared to violation items. Consequently, they remembered the specificity of non-violation items that violated the task structure better than violation items.

Furthermore, our findings on violations leading to lower memory specificity in children compared to non-violation items may have implications for understanding the role of curiosity in memory enhancement. Curiosity is known to promote learning and memory by making knowledge gaps more relevant and engaging individuals with new information (for a recent review, Gruber & Ranganath, 2019). However, violations can potentially diminish curiosity in children, particularly when they generate cognitive conflict (Brod et al., 2020). Violations disrupt predictability and coherence, potentially reducing intrinsic motivation to explore and remember information associated with the violation. Therefore, in our study, children may exhibit lower memory specificity for violating items as their curiosity and interest in violations are not effectively engaged. The benefits of prediction generation depend on children's inhibitory capacities to effectively use cognitive conflict to revisit their previous knowledge and update it (Brod et al., 2020). In our task, it is possible that violation items did not elicit a curiosity process since they merely represented deviations from what was predicted earlier. Consequently, there was no perceived need or motivation to update the previously learned associations. In contrast, non-violation items might be evaluated as more informative than violation items as they are inconsistent with the previously learned task structure, which might explain why they elicited curiosity and led to better memory specificity. Taken together, it can be concluded that further investigations are needed, particularly exploring the impact of PE on curiosity, inhibition, and memory processes to better understand the observed differences in children who were better to dissociate non-violation items.

3.4. Limitations and Future Directions

The presented work possesses several limitations that should be acknowledged. First our research designs lack the ability to sufficiently motivate participants to update their predictions. Despite demonstrating methodological rigor, such as encoding ratings in Study 1, participants were only exposed to PE without any subsequent actions that would prompt them to update their internal models or revisit the events that elicited PE. The lack of perceived importance or relevance for future tasks may have hindered participants' motivation to engage in updating processes. Second, our task structures align with traditional memory studies, which involve participants studying lists of items and aiming for direct recall (following the principles of Ebbinghaus (1885)). Recent discussions emphasize the importance of adopting a more naturalistic approach in memory research to gain a deeper understanding of how memory functions in real-world contexts (Ranganath, 2022). In order to understand how the brain encodes and retrieves PE, researchers could focus on more naturalistic approaches rather than having a clear distinction when and how to process the events (Lu et al., 2022). Lastly, incorporating more comprehensive methods, such as decoding the EEG signal, could provide more valuable insights into the underlying neural mechanisms of PE (Postle, 2016). Previous research revealed that decoding the signal of expected stimulus even before the onset is possible (Kok et al., 2017). In a similar vein, researchers could decode neural signals associated with expected and unexpected events, providing specific neural patterns to understand the representations of PE. Future research aiming to investigate the impact of PE on episodic memory could address these issues to enhance the validity and generalizability of the findings.

3.5. A Metascientific Perspective on The Relationship Between PE and Episodic Memory

Overall, our findings did not replicate [6] previous research showing the memory-enhancing effect of PE (e.g., Bein et al., 2021; Brod et al., 2018; Kafkas & Montaldi, 2018; Quent et al., 2022). The replication crisis in psychology research has garnered significant attention, prompting more transparent practices such as pre-registration and openly sharing methods, data, and analysis scripts. While we adhered to these recommendations in all our studies, it is evident that these steps alone may not suffice in addressing the replication problem. One potential contributing factor to the replication crisis lies in the limitations of existing theories in psychological research (Szollosi & Donkin, 2021). Importantly, this concern has longer traditions than the replication crisis itself (i.e., theory crisis in psychology, Meehl, 1978; Newell, 1973). In the presented work, we adopted the predictive processing framework (Bar, 2007; Friston, 2010; Knill & Pouget, 2004), which postulates that PE leads to enhanced memory. However, our results repeatedly indicated that this explanatory power of the framework may not be readily replicable, as it appears to be more complex and contingent on moderating factors. Nevertheless, adhering to open science practices is a strength of the presented dissertation, it allows us to reveal the challenges associated with replicating the PE effect. We believe that our work has provided valuable insights into the advancement of scientific knowledge within this field.

It is important to emphasize that, in terms of scientific knowledge growth, which differs from mere accumulation of observations (Popper, 1963), our results can be viewed as anomalies within the predictive processing theory with Kuhn's terminology. Anomalies refer to observations that deviate from what is predicted by a prevailing theory (Kuhn, 1970). The identification and analysis of anomalies play a crucial role in scientific inquiry as they can lead to the refinement of theories, or even paradigm shifts in a field of study. The presented results failing to replicate previous findings have prompted critical discussions regarding the conditions under which PE influences memory. Our primary objective was to move closer to a comprehensive explanation of the relationship between PE and episodic memory. Otherwise, the explanatory power of the predictive processing framework may fall short, rendering it merely a proof-of-concept exercise rather than a framework that can be applied across various studies in psychology and neuroscience research. On the other hand, it should be noted that the

[6] Here, the term replication was used to describe the degree to which the consistent predictions of a theory can be observed across multiple testing instances, rather than repeating a study under the same or similar conditions.

pursuit of understanding complex cognitive functions such as memory and PE, as well as their relationship, is undoubtedly challenging. However, it remains a promising endeavor. Researchers can draw inspiration from successful explanations of other complex systems, such as evolution and natural selection (Szollosi & Donkin, 2021). These examples give researchers hope that the pursuit should not be abandoned. Answers to the complex questions, like how the brain works, emerge through experience. We must first attempt to test explanations, acknowledge results, learn from them, and persist in our efforts. In conclusion, we believe that our results remain fruitful, as they open avenues for new explorations. Our insights into the relationship between PE and episodic memory have expanded through these findings, which have presented us with novel problems to solve.

3.6. Concluding Remarks

The presented dissertation aimed to understand the relationship between PE and episodic memory. By means of the presented work, we gained insights on the following matters that are important to highlight: (i) the effect of PE on memory benefit is not systematic as previously postulated (In Study 1, 2, & 3). (ii) Study 1 suggests that events which are in line with our predictions are remembered better compared to events eliciting PE. (iii) Study 2 highlights the importance of recollection process as a possible moderator for the relationship between PE and episodic memory. (iiii) Study 3 showed that children can benefit from violations of the context. We believe that these findings advance our understanding of the complex interplay between PE and episodic memory. That is, the notion that PE is a driver of new learning and a possible reason for better memory may not direct as previously postulated.

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Original Manuscripts

Original Manuscripts – Study 1

From generating to violating predictions: The effects of prediction error on episodic memory

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Data, scripts, and additional online materials are openly available at the project's Open Science Framework page (https://osf.io/pfgyb/). We have no conflicts of interest to disclose. The study was funded by a Starting Grant from the European Union for YLS (ERC-2018-StG-PIVOTAL-758898). The work of YLS was also supported by the German Research Foundation (Project-ID 327654276, SFB 1315, "Mechanisms and Disturbances in Memory Consolidation: From Synapses to Systems"), and the Hessisches Ministerium für Wissenschaft und Kunst (HMWK; project "The Adaptive Mind"). The work of SN was also supported by a Research grant Focus A/B, Goethe-University Frankfurt am Main, ("Dynamics of auditory and visual memory representations in the aging brain").

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Abstract

Generating predictions about environmental regularities, relying on these predictions, and updating these predictions when there is a violation from incoming sensory evidence are considered crucial functions of our cognitive system for being adaptive in the future. The violation of a prediction can result in a prediction error (PE) which affects subsequent memory processing. In our preregistered studies, we examined the effects of different levels of PE on episodic memory. Participants were asked to generate predictions about the associations between sequentially presented cue-target pairs, which were violated later with individual items in three PE levels, namely low, medium, and high PE. Hereafter, participants were asked to provide old/new judgments on the items with confidence ratings, and to retrieve the paired cues. Our results indicated a better recognition memory for low PE than medium and high PE levels, suggesting a memory congruency effect. On the other hand, there was no evidence of memory benefit for high PE level. Together, these novel and coherent findings strongly suggest that high PE does not guarantee better memory.

Keywords: prediction error, episodic memory, predictive processing

Introduction

According to the predictive processing framework (Bar, 2007; Friston, 2010; Henson & Gagnepain, 2010), key functions of the cognitive system are to generate predictions about environmental regularities and to update these predictions when there is a violation from incoming sensory evidence, giving rise to a prediction error (PE). Building up abstracted knowledge can be achieved by extracting the statistical regularities of the environment. The violation of the abstracted knowledge can result in a PE. It may be important to remember these events giving rise to PEs to ensure better predictions in the future.

The memory benefit of events giving rise to PE has been demonstrated in a series of recent studies (Bein et al., 2021; Brod et al., 2018; Greve et al., 2017; Kafkas & Montaldi, 2018; Quent et al., 2022). When we encounter an event that gives rise to PE, we tend to remember it better, possibly because it can be important for improving our predictions in the future. For example, to investigate the memory benefit for such events, Kafkas and Montaldi (2018) used a rule learning task in which participants learned a contingency relationship between six different symbols and two stimulus categories, i.e., natural or human-made. Then, they violated the previously experimentally-induced relationships either in memory encoding or retrieval phases. Their results showed that the presentation of unpredicted stimuli enhanced the subsequent recollection performance regardless of the position of the violation (i.e., at memory encoding or retrieval).

On the contrary, another body of research has shown that events that are in line with our predictions are remembered better, i.e., the memory congruency effect (Alba & Hasher, 1983; Anderson, 1981; Craik & Tulving, 1975). For example, congruent associations (e.g., wood-chair) would be easier to remember than incongruent associations (e.g., wood-cookie). This account has been largely corroborated by recent behavioral evidence, e.g., in studies with item-scene pairs (Brod & Shing, 2019; Liu et al., 2018; Ortiz-Tudela et al., 2017; van Kesteren et al., 2013), item-location pairs (Atienza et al., 2011) and non-preexisting relations (Ostreicher et al., 2010).

To bridge these diverging findings in the literature, a recent model called Schema-Linked Interactions between Medial Prefrontal and Medial Temporal Lobe (SLIMM, van Kesteren et al., 2012) suggests a U-shape relationship between prediction and memory, in which different brain systems are involved. The model postulates that memory benefit is proportional to the degree of PE, where the degree is calculated via the difference between the prediction and the actual outcome. That is, events that are correctly predicted (i.e., low

PE) would lead to better memory, as the memory congruency effect suggests (Brod et al., 2013), and this process is supported by the medial prefrontal cortex (mPFC). By means of the mPFC, already existing connections between representations upon which predictions are built become strengthened, facilitating the retrieval of the respective information. Similarly, events giving rise to PE (i.e., high PE) would also improve learning and memory (Henson & Gagnepain, 2010). The model postulates that the medial temporal lobe (MTL) creates "snapshots" for those events, resulting in a memory advantage. Lastly, events that are neither strongly predicted nor unpredicted would lead to medium PE. Since the activation of mPFC and MTL is weak for those events with medium PE, they would not benefit memory. Taken together, the varying differences between predictions and actual outcomes would result in low, medium, to high PE levels, which in turn is postulated to exhibit a U-shape relationship with episodic memory: Events of two ends of PE, namely low and high PEs, are assumed to be remembered better compared to medium levels.

A recent study by (Greve et al., 2018) showed evidence for this U-shape function. In their series of experiments, the authors first led their participants to learn a rule about the pairing of object exemplars, which was then manipulated in three levels based on the strength of matching level with previous learned associations, namely, congruent, incongruent, and unrelated. While the rule remains unchanged for the congruent level, the incongruent level has a reversed rule. On the other hand, for the unrelated level, the rule reversed after the first trial. The authors aimed to establish a rule about the paired objects and subsequently violate or confirm them on the critical trial just before testing memory performance. Importantly, for the unrelated level, there was no rule to establish. Even though their results were in line with the U-shape function, it should be noted that the medium level was unrelated to the previous learned associations. One can argue that the poor memory performance for the medium level might be related to the requirement to create new associations instead of representing the medium level in the spectrum.

Another study from the same group of researchers (Quent et al., 2022) addressed this issue via a continuous function of prediction. The authors conducted a virtual reality study in which participants had to explore a virtual kitchen with kitchen objects positioned in different locations which had varying degrees of congruency based on semantic predictions. For example, kettle placed at the counter would be predicted (low PE), kettle placed at table would be neither strongly predicted nor unpredicted (medium PE), and kettle placed at trash can would be unpredicted (high PE). The authors used both recall and an alternative forced-choice task to test subsequent memory for the object-location pairs. Their results followed the U-shape function of PE, suggesting better memory for predicted and unpredicted events when compared to the medium level. On the other hand, the authors also pointed out that it remains unknown to investigate the U-shape function when predictions are driven from an episodic context rather than pre-experimental knowledge (Ortiz-Tudela et al., 2021).

We aimed to address the issue of the two conflicting ends of the U-shape, i.e., the memory congruency effect and the boosting effect of PE, in an episodic memory context. Importantly, previous studies that showed the benefits of PE on subsequent memory were either missing a medium level (Kafkas & Montaldi, 2018) or their medium level was unrelated to experimentally-induced associations (Greve et al., 2018). In our two preregistered studies, we attempted to address this issue by creating a medium level that was being related to the previously induced prediction learning. We asked our participants to learn associations between cue-target pairs (i.e., Experiment 1: musical instrument sound and object categories; Experiment 2: environment and item categories) and to generate predictions based on these associations. Hereafter, we violated their predictions with individual items in three PE levels, low, medium, and high, respectively. The subsequent memory for the individual items and their associations were assessed. We expected that this paradigm would help us to test the U-shape function of PE as a continuum, with the medium level related to experimentally induced prediction learning. Testing the SLIMM model with these two preregistered studies that were meant to be conceptual replicates of each other, we hypothesized that there is a U-shape relationship between PE level and recognition memory performance. We further hypothesized that low and high PE levels would have better recognition memory in comparison to medium PE level. Moreover, we expected that performance on the association test varies as a function of PE and there is a significant difference between confidence ratings across different PE levels.

Experiment 1

Experiment 1 sought to test the U-shape function of different PE levels on recognition memory using associations between auditory and visual stimulus categories. During the first day, participants were presented with sounds of musical instruments and asked to predict the upcoming object category which can be either natural or human-made. More importantly, the musical instrument categories predicted the object categories in varying degrees (please see Figure 1D). In line with the study from (Schapiro et al., 2012), repeated pairing of associations would enable one to generate better predictions over time, through statistical learning. On the second day, they were again presented with sounds of musical instruments and asked to predict the upcoming object category in their mind based on what they have learned on the previous day. After their prediction, individual objects were presented to create three levels of PE, low, medium, and high PE. It should be noted that three levels of PE were not only based on the varying levels of contingency, but also on categorical differentiation which comes from subcategories of natural and human-made objects (see Procedure section below for details). A surprise memory task followed the encoding phase in which item memory for the objects and associative memory for the object-sound pairs were tested.

Method

Participants

60 participants (46 females, aged 18–29 years, mean age = 21.92 (SD = 2.84)) were recruited for the study. They were recruited through advertisements across the campuses of Goethe University of Frankfurt, student social media groups, and Prolific (https://www.prolific.co/). For their compensation, participants received either course credits or eight € per hour. All participants had normal or corrected-to-normal vision and hearing. Participants who reported a history of neurologic or psychiatric disorder were excluded from participation. They all signed an informed consent approved by the local ethics committee of the Goethe University Frankfurt before their participation. The study design and analyses were preregistered on the Open Science Framework (https://osf.io/wybtn) before data collection.

Since the main aim of the study was to understand the effect of PE on recognition memory, an absence of generating accurate predictions on the associations between object and sound categories would make the memory results difficult to interpret. Therefore, in line with our preregistration, we decided to exclude participants with poor learning performances of less than a 65 % accuracy rate. Ten participants who could not reach the criterion were excluded from the further analysis steps.

Material

The stimuli consisted of sounds of musical instruments and object pictures. The sounds of musical instruments were selected from four categories: guitar, trumpet, violin, and piano with eight distinct sounds per category. A total number of 196 object pictures was selected from the BOSS database (Brodeur et al., 2014). The objects were equally divided into two main object categories, natural and human-made, with two sub-categories each. For natural objects the sub-categories consisted of animals and fruits/vegetables/nuts, for human-made objects the sub-categories consisted of household and toys/school/sports objects.

Procedure

The study was conducted over two sessions taking place on two consecutive days and lasting one hour each (see Figure 1). On the first day, participants were trained to learn the sound-object category associations to build up predictions. On the next day, they were asked to complete encoding and recognition phases. Since the study took place online due to the pandemic, we implemented additional steps into the data collection procedure to gain traction on data quality (Newman et al., 2021). Each session started with a video call with the participant to check their overall well-being and physical environment. All participants were informed that they must be in a quiet room, sitting in a comfortable chair, using a computer with a stable internet connection, and to minimize distractions to be able to focus on the task. Also, we subdivided each task into several blocks and suggested our participants to take short breaks in between. The information about online testing was followed by the task instructions. The instructions were given in both spoken (during the video call) and written form (during the task). Once the participant completed the task, they were asked to video call the experimenter again to give feedback about their participation and talk about any unforeseen problems that might resulted in the incompletion of the task. In addition to the video call, they were strongly encouraged to watch the video prepared by our team to get familiarized with online testing prior to the study (https://www.psychologie.uni-frankfurt.de/102061001/Instructions_for_Online_Testing___English_Version). The presentation of stimulus and response collection were programmed in PsychoPy v2021.1.4 and https://pavlovia.org was used to run the task (Peirce, 2007).

Prediction Learning Phase. The prediction learning phase served to build up predictions about the sound-object category associations (see Figure 1A). For each of four sound categories, there were one strongly (70 %), one mildly (20 %), and two weakly (10 %) associated object categories. Most importantly, strongly and mildly associated categories were derived from one of the main categories, namely natural or human-made. Figure 1D demonstrates an example of the structure of the association between sound and object categories. In the figure, guitar sounds were strongly associated with animals. Consequently, whereas the mild association was fruits/vegetables/nuts, the weak associations were human-made categories.

During the task, participants were asked, after hearing the sound, to predict the upcoming object category. The contingency structure of the task was unknown to participants, and they had to learn the associations across trials. Each trial started with a fixation cross at the center of the screen for 1000 ms and was followed by the sound for 3000 ms. Participants were then asked to predict the category of the upcoming object based on two levels, natural or human-made. After their response, an object from the sixteen exemplars was presented for 3000 ms following the designated contingencies. Although the category prediction task was self-paced with no time limit, participants were encouraged to be as fast and accurate as possible. All participants completed 200 trials equally spread over five blocks. The association between sound and object categories was counterbalanced across participants to keep the sub-category structure stable.

Encoding Phase. The second session of the study took place approximately 24 hours after the first session and started with the encoding phase (Figure 1B). In this phase, we aimed to violate predictions with individual object pictures which have not been presented before. The following contingencies were used: 50 %, 30 %, and 20 % for strongly, mildly, and weakly associated pairs, respectively, to maintain the original contingencies as close as possible to the prediction learning phase while increasing the number of trials possible for the weakly associated category. As in the prediction learning phase, the strongly and mildly associated categories were derived from one of two main object categories.

Each trial started with a fixation cross at the center of the screen for 1000 ms and the musical instrument sound was presented for 3000 ms. After hearing the sound, participants were presented with a blank screen and asked to predict the most likely object category in their mind for 2000 ms. More importantly, they were previously informed about the four different object categories, namely, animals, fruits/vegetables/nuts, household, and toys/school/sports objects, and were instructed to predict one of those categories. Participants were informed about the four object categories on Day 2 because it was aimed to create medium PE level via varying levels of contingencies and semantic subcategories. The paired object picture was presented for 3000 ms. Then, participants were asked to indicate whether the presented object belongs to the same category which they predicted based on a 4-level Likert scale (from 1: Strongly yes to 4: Strongly no). The encoding phase consisted of three blocks of 40 trials, for a total of 120 trials.

Recognition Phase. Immediately after the encoding phase, a surprise recognition phase started (Figure 1C). In addition to the 120 object pictures from the previous phase, 60 new objects were included. The new objects were equally selected from the four object categories. Each trial started with a fixation cross for 1000 ms and was followed by the object picture presentation for 3000 ms. Participants were required to give an old/new judgment and to provide their confidence based on a 4-level Likert scale (from 1: very sure to 4: very unsure). Hereafter they were asked to select the sound (between two options) that was associated with the presented object. They listened to two sounds one after another and indicated which one was paired with the object. To avoid guessing biases based on the previously learned associations, the alternatives were selected from the same musical instrument category. All responses were self-paced with no time limit. A total of 180 trials was distributed across three blocks.

Statistical Analyses

To test the effect of PE levels on recognition memory performances, we assessed the participants' hit responses based on correct answers for old items. Before testing the main hypothesis, cumulative accuracy scores were computed to exclude participants with poor learning performances (below 65 %). Also, mean prediction rates from the encoding phase were assessed as a sanity check for our PE manipulation. For all phases of the study, trials with reaction time shorter than 100 ms or longer than 1500 ms were excluded.

To determine whether PE level was a significant predictor of recognition memory performance, we conducted a linear mixed effect model with participant as random intercept to account for between-participant variability in hit responses. The model included PE level (low, medium, and high PE) and confidence ratings (from 1: very sure to 4: not unsure) as fixed within-participant factor. Model estimations were determined with maximum likelihood ratio and the statistical significance of the fixed effects was determined using $\chi 2$ (chi-squared) tests. In addition to our primary analyses on the effect of PE level on hit responses, we also analyzed the responses for the associated sound pair with the same model specification. All analyses were performed using custom-made R scripts with the lmer function in the lme4 package (Bates et al., 2015) that can be found on the OSF page (https://osf.io/pfgyb/).

In addition to our primary hypothesis of mean differences across PE levels, we also exploratorily analyzed the relationship between learning, PE, and recognition performance. Assumingly, participants whose learning performance was better would benefit more from high PE compared to participants with lower learning performance. We assessed learning performance via cumulative accuracy from the last third of trials from the prediction learning phase. A linear mixed effect model was calculated with participant as random intercept. We included learning performance and PE level as fixed factors into the model.

Deviations from the registered protocol

The current study was preregistered prior to the data collection (https://osf.io/wybtn) and there are some deviations from it which are important to mention (Claesen et al., 2021). Firstly, even though we planned to test 45 participants assuming an effect size of .25 to observe .80 power, additional participants had to be recruited due to problems related to exclusion criteria, online testing and failed data transmission. The second main difference from the preregistered plan was in the encoding phase. We had planned to ask our participants to report the category of the presented object (e.g., animal or fruit). However, during the pilot studies, it revealed that participants were not attentive to the associations between sounds and objects, since attending the object only would be sufficient to solve the task which was selecting its category. Therefore, generating different PE levels for associations between sound and object categories was not possible although it was crucial for the study. We correspondingly decided to update the encoding phase in which participants indicated if the presented object belongs to the same category which they predicted. Lastly, the preregistered plan was to test hypotheses with a within factors repeated measures ANOVA. We changed our statistical model to a linear mixed model because it allows us to control for the variance attributed to random factors (e.g., participants) and it was more suitable for an unbalanced number of observations since in the present study the number of trials differed among PE levels due to the nature of the experimental design.

Results

First, to check if participants generate predictions about the sounds of musical instruments and object categories, we examined the accuracy results from the prediction learning phase. Mean accuracy across participants was .87 (SD = .33) during the prediction learning phase that was significantly above chance levels of performance ($t(49) = 28.75$, $p < .001$, $d = 4.07$). Figure 3A shows that the accuracy of predicting the upcoming object category increased with trials. This shows that participants could generate predictions about the associations between musical instruments and object categories.

Then, to test our manipulation on the PE levels, participants' category judgments during the encoding phase were investigated. Ratings about the distance between the presented object category and the category they previously predicted were collected. While the highest ratings (i.e., 4- Strongly no) mean that the presented object did not belong to the same category that participants predicted earlier, the lowest ratings (i.e., 1- Strongly yes) indicate that the presented object was from the same category that they predicted. The results can be seen in Figure 3B. The model for the encoding phase with participant as random intercept and PE level as fixed factor showed that there was a significant main effect of PE ($\chi^2(2) = 292.3$, $p < .001$), indicating that higher ratings were obtained for high PE trials ($\beta = 1.98$, $t = 16.88$, $p < .001$) and medium PE trials ($\beta = .56$, $t = 5.76$, $p < .001$) compared to low PE trials. This result indicates a strong verification for our manipulation on the PE levels, such that our participants reported that objects from high and medium PE levels are not from the category they predicted.

The model to predict recognition memory performance for PE levels with participant as random intercept indicated a significant main effect of PE ($\chi^2(2) = 8.27$, $p = .02$). Post-hoc contrasts showed that hit responses for high PE levels ($\beta = -.24$, $z = -2.79$, $p = .01$) were lower than low PE level (see Figure 3C). In addition to PE level, we added confidence ratings as fixed effect for random intercept and random slope into the model and compared both models. The model fit was significantly improved, $\chi 2(81) = 871.58$, $p < .001$; AIC first: 6293.6, second: 5584.1. The main effect of confidence ($\chi^2(3) = 169.08$, $p < .001$) was significant, indicating higher hit responses obtained at the highest confidence rating (1- Very sure) compared to the other confidence ratings (2- Sure: $\beta = -1.77$, $z = -6.89$, $p < .001$; 3- Unsure: $\beta = -2.78$, $z = -9.18$, $p < .001$; 4- Very unsure: $\beta = -3.42$, $z = -8.99$, $p < .001$). The interaction effect between PE and confidence was significant ($\chi^2(6) = 12.91$, $p = .04$), which indicated that participants' hit responses were lower for high PE level compared to low PE level at lower confidence ratings (3- Unsure: $\beta = .81$, $z = 2.57$, $p = .01$; 4- Very unsure: $\beta = 1.08$, $z = 2.37$, $p = .02$). The results can be seen in Figure 3D. Lastly, we applied a similar model to test the association memory accuracy. There was neither significant main nor interaction effect of PE level on association memory accuracy, $\chi 2(2) = 1.90$, $p = .45$.

We further tested our exploratory question about the relationship between learning, PE, and recognition memory. The model was run to predict recognition memory performance with PE levels and cumulative accuracy scores with fixed effects and participant as random intercept. Results showed significant main effect of PE ($\chi^2(2) = 8.40$, $p = .02$). Post hoc comparisons indicated that highest hit responses were measured for low PE level ($\beta = .75$, $t = 4.87$, $p < .001$). Neither the effect of learning nor the interaction was significant.

Discussion

Experiment 1 showed that while three levels of PE were successfully constructed during the encoding phase by generating predictions about the associations between sound and object categories in the prediction learning phase, the hypothesized U-shape function of PE on recognition memory was not observed. In contrast, our results indicated that recognition memory was better for low PE than high PE, suggesting a memory congruency effect. As one can argue that the U-shape function of PE is observable mostly for associative memory because of its role in creating "snapshots" for high PEs (Henson & Gagnepain, 2010), we also assessed associations between individual items and their sound pairs, but we did not observe a memory benefit for high PE. Even though these findings provide contradicting evidence for the U-shape relationship between PE and memory, it is crucial to rule out that the absence of this PE effect might be linked to the task-related differences. For example, we argue that it should be revisited how predictions are experimentally built up. It is very likely to make a difference if pre-experimental knowledge (i.e., semantic categories) is used or certain contingency structures are established during the prediction learning phase. In other words, in Experiment 1, the contingency structure that was built up during the very first phase of the study with varying degrees of PE was also based on semantic categories of the objects. The issue with this task structure might be that participants were not sensitive to the individual items shown during the encoding phase because participants had been acquainted with being presented with objects which were from different semantic categories than their predictions. Experiment 2 sought to address these issues.

Experiment 2

Experiment 2 followed the same rationale as Experiment 1: Testing the U-shape function of PE on memory with all levels based on experimentally-induced prediction learning. However, there are three main differences between our two experiments worthwhile highlighting. First, due to the nature of Experiment 1, the PE levels were based on semantic sub-categorization (e.g., animals and fruits/vegetables/nuts for the natural object category). We aimed to rule out any potential effects of previous semantic knowledge by using associations between artificial creatures called "Wubbels" and their environments in Experiment 2 (Watson et al., 2019). Secondly, in Experiment 1, varying contingencies started from the very first phase (i.e., the prediction learning phase). During the prediction learning phase, the musical instrument categories predicted the object categories to varying degrees, thus this setup might have resulted in participants having the understanding that their predictions can be sometimes incorrect. As a consequence, participants might not have been sensitive to medium and high PE trials during the encoding phase, because they already knew from the first phase that sometimes the presented object does not match with their predictions. Therefore, in Experiment 2, we decided to have a deterministic prediction learning phase in which the contingency was set to 100 %. Lastly, in Experiment 2 we measured two additional aspects of associative memory, i.e., Wubbel-scene pair and Wubbel-location pair (see Procedure section for details).

As in Experiment 1, the study consisted of three phases: Prediction learning, encoding, and recognition (see Figure 2). In the prediction learning phase, participants were asked to learn Wubbel-scene associations via feedback across trials. During the encoding phase, they were presented with individual, unique Wubbels that varied to certain degrees to create three PE levels. In the end, recognition and associative memory were assessed to test the U-shape function of PE on memory.

Method

Participants

51 participants (28 females, aged 18-35 years, mean age = 23.14 (SD = 4.49)) were recruited in this study. They were recruited through advertisements across the campus, student social media groups, and Prolific (https://www.prolific.co/). The inclusion criteria were having normal or corrected-to-normal vision and hearing. Participants with a history of neurologic or psychiatric disease were not recruited for the study. All participants signed an informed consent approved by the local ethics committee prior to their participation and they were given either course credits or honorarium for their compensation. The preregistered study design and analyses can be found in the Open Science Framework (https://osf.io/bwujz). With the same rationale as in Experiment 1, we excluded one participant from the analysis due to poor learning performance with a less than 40% accuracy rate.

Material

We used associations between the artificial creatures called "Wubbels" and certain environments to prevent the effect of prior knowledge (Watson et al., 2019). The scenes for environments were selected from the ECOS database (https://sites.google.com/view/ecosdatabase/) with four distinct categories: beach, snowy mountains, desert, and savannah. There were four different exemplars for each environment category.

The Wubbels were created with the Autodesk 3DS Max software using the provided script by Watson et al. (2019). The creation of Wubbels followed a schema according to which the main feature defining the affiliation with one of the two species is the body shape, i.e., longish or roundish. The body shapes of the four Wubbel families were consistent with their primary species. That is, families one and two, which are affiliated with the *long-shaped* species, have *concave* and *oblong* body shapes, whereas families three and four, which are affiliated with the *round-shaped* species, have compressed *oblong* and *spherical* body shapes (see Figure 2D). We structured Wubbels into two main groups, the so-called Wubbel parents and Wubbel children to use them during the prediction learning and the remaining phases (i.e., encoding and recognition), respectively.

The main difference between Wubbel parents and Wubbel children was that the children have varying features. Except for the Wubbel parents, i.e., the prototype pairs used for the prediction learning phase, the additional features of the Wubbel children, such as hat shape (6 instances), arm shape (4 instances), skin type (6 instances), body color (13 instances), pattern color (13 instances), and pattern (50 instances) were variable. They were attached to the body strategically to ensure that the Wubbels are as dissimilar from another as possible. To this end, a matrix with all possible feature combinations was built from which 80 combinations with a distance of at least three features were randomly drawn. The drawn combinations provided the building instructions for the Wubbels. That is, we aimed to guarantee that at least three features do not overlap when one compares all Wubbels to one another. This procedure resulted in a set of 80 unique Wubbel children which were used in the encoding and recognition phases. In contrast to the Wubbel children, the parents differ as the assigned color patterns are for one prototype vertically striped and for the other prototype horizontally striped rainbow colors, respectively. Similarly, as for the Wubbel children, each prototype had a unique combination of the remaining features complementing its body. All color and pattern patches were created with Python 3.7.4 using the OpenCV library.

Procedure

There were three study phases on two consecutive days and each lasted for one hour. On day 1 in the prediction learning phase, participants learned associations between Wubbels and environments. The second session on day 2 started with the encoding phase and was followed by the recognition phase. This study was also run online. Therefore, we followed the same structure as in Experiment 1 including the video call with participants in order to increase data quality. The presentation of stimulus and response collection were programmed in PsychoPy v2021.1.4 and https://pavlovia.org was used to run the task.

Prediction Learning Phase. The purpose of the prediction learning phase was to let participants learn the Wubbel-environment associations to be able to generate predictions. The phase started with a cover story in which the Wubbels, their species, and their families were introduced. Participants were told that each Wubbel family lives in a different environment and they were asked to learn these combinations as quickly as possible (Figure 2A). There were two prototypes for each four families and four scene pictures for each four scene categories. The associations between Wubbels and environments were predetermined, and the contingency was 100 %.

Each trial started with a scene and a fixation cross in the center for 500 ms. Then, two Wubbels from different families were presented in two out of four possible screen locations (i.e., top-right, top-left, bottom-right, and bottom-left). Here, participants were asked to decide which Wubbel matches with the presented scene by giving a response. After their response, feedback was presented via a green (correct) or red (incorrect) frame around the chosen Wubbel according to the pre-determined associations based on 100 % contingency for 3000 ms. The prediction learning task was self-paced with no time limit, but we encouraged our participants to be as fast and accurate as possible. The total number of trials was 96 for one block. The associations between Wubbels and environments were counterbalanced across participants.

Encoding Phase. The second session started with the encoding phase approximately 24 hours after the first session (Figure 2B). To create three different levels of PE, individual, unique Wubbel pictures, which we told the participants as Wubbel children, were used. We used twelve Wubbel-children for each family and divided them into three conditions, low, medium, and high PE levels. In detail, a Wubbel child shown in an environment of its own family would elicit a low PE, a Wubbel child from a different family but within the same species would lead to a medium PE in that same environment, and a Wubbel child from the other species would lead a high PE. As in the example presented in Figure 2, participants learned in the prediction learning phase that one family prototype of the long-shaped Wubbel species lives on the beach. When a child from this family was presented with a beach during encoding, it would lead to low PE because participants would have expected to find a family member with such a longish body shape. When the same child was presented with an environment category associated with the other long-shaped family, i.e., a desert, it would result in medium PE level. Lastly, presenting the same child with any environment associated with a round-shaped family, i.e., a savannah, would create high PE.

Prior to the task, participants were first instructed about the structure of Wubbel families and their children. It was explained that the children have the same body shapes as their parents and that they are similar to their relatives as they have similar body shapes (please see Figure 2D). It was also described that they are very different from the other two unrelated families who have very different body shapes. Moreover, they were told that they can see them in different environments since the children of Wubbels always visit each other because they enjoy meeting other Wubbels. The contingencies for PE levels were equal, meaning twelve Wubbels for each PE level. The participants' task was to indicate the matching level between Wubbels and the environments.

Each trial started with a fixation cross at the center of the screen for 500 ms and a scene was presented for 3000 ms. During the scene presentation, participants were asked to predict the most likely Wubbel family in their minds based on what they have learned the day before. Then, a Wubbel child was presented on one out of four possible screen locations for 3000 ms. Participants were asked to indicate whether the presented Wubbel child belongs to the same family which they predicted or not, using a 4-level Likert scale (from 1: Strongly yes to 4: Strongly no). This was followed by a 2500 ms blank screen to wait for the next Wubbel child. The total number of trials was 48 and the association structure from the previous day was the same. Different from Experiment 1, we told participants that there will be a memory test for the Wubbel children, their features, the environment as well as the location on the screen they were shown at. Thus, whereas Experiment 1 was incidental, this study was based on intentional learning.

Recognition Phase. The recognition phase followed the encoding phase (Figure 2C). The Wubbels from the previous phase were presented with 32 new Wubbel children - eight from each family. Each trial started with a fixation cross for 500 ms. Then, participants had to indicate whether they have seen the presented Wubbel before or not and rate their confidence based on a 4-level Likert scale (from 1: very sure to 4: very unsure). Regardless of their response, scene association and scene location tasks were employed for old Wubbel children. Participants had to choose the correct scene from four alternatives. Importantly, the alternative scenes were from the same scene category to prevent guessing biases. Lastly, participants were asked in which location on the screen the Wubbel was presented. All responses were self-paced with no time limit. All participants completed 80 trials.

Statistical Analyses

The steps for statistical analyses were identical to Experiment 1.

Deviations from the registered protocol

Our preregistered study and analysis plan can be found here: https://osf.io/bwujz. Due to unforeseen reasons, we had to deviate in several aspects during the study, with the reasons being summarized here. As in Experiment 1, due to problems related to online testing, we had to test more participants than we originally reported. The initial sample size was 40 to obtain .80 power with an effect size of .40 at the standard .05 alpha error probability. During the pilot task, Wubbels had two main features, namely body shape, and color. However, it had not been anticipated that the color information overshadowed body shape information, as a consequence, participants considered solely the body shape information to accomplish the task. Unfortunately, we could not create the different levels of PE even though it was our main manipulation of the task. Thus, we decided to only have the body shape as the main characteristics to define species but not color information. The other important deviation was to have a different structure for the encoding phase. The pilot task with the like/dislike task did not show significant difference in PE levels. Therefore, we changed the structure and asked participants to evaluate if the presented Wubbel matched with the scene. The last deviation concerned the analysis plan. Similar to Experiment 1, we decided to run linear mixed models instead of repeated measure ANOVA due to the aforementioned reasons.

Results

We first checked prediction learning performance during the first phase. Mean accuracy across participants was .88 (SD =.32) which was significantly above chance levels of performance ($t(50) = 29.34$, $p < .001$, $d = 4.11$). As in Experiment 1, learning performance for the associations between Wubbels and scene categories increased with trials indicating that participants were able to generate accurate predictions (Figure 3A). Then, we tested the effect of PE level on the category judgments in the encoding phase (Figure 3B). The results showed a main effect of PE, $\chi^2(2) = 690.66$, $p < .001$. The ratings were higher for high PE trials ($\beta = 2.39$, $t = 25.83$, $p < .001$) and medium PE ($\beta = .96$, $t = 10.58$, $p < .001$) compared to low PE. Together with these results, we further supported our PE manipulation.

As in Experiment 1, the model to predict hit responses for PE levels with participants as random intercept showed a significant main effect of PE ($\chi^2(2) = 13.63$, $p = .01$). Post-hoc comparisons indicated that hit responses for high PE level were lower than low PE level, $\beta = -.36$, $z = -3.23$, $p = .01$. Results can be seen in Figure 3C. Next, we continued by adding confidence ratings to the model. The model fit was significantly improved, $\chi 2(81) = 153.36$, $p < .001$; AIC first: 3173.2, second: 3181.8. The main effects of PE level ($\chi^2(2) = 9.30$, $p = .01$) and confidence ratings ($\chi^2(3) = 8.24$, $p = .05$) were significant but there was no interaction effect, $\chi 2(6) = 5.28$, $p = .51$. Post hoc comparisons only showed that higher hit responses were recorded at rating level 2- Sure, $\beta = .53$, $z = 1.77$, $p = .07$ (Figure 3D). Neither the results for association memory for scene pair ($\chi 2(2) = 2.94$, $p = .23$) nor the results for association memory for location ($\chi 2(2) = .02$, $p = .99$) indicated a main effect of PE level.

For our exploratory analysis, the mixed-effect logistic regression to predict recognition memory performance for different PE levels and cumulative accuracy scores from the prediction learning phase indicated that there was a significant main effect of PE ($\chi^2(2) = 12.14$, $p < .01$). Post hoc comparisons indicated that hit responses for high PE levels ($\beta = -.01$, $t = -.02$, $p = .02$) were lower than for low PE levels. Neither the effect of learning nor the interaction was significant. These findings demonstrate that beyond the proxy of recognition memory, better performances were obtained at low PE compared to high PE level, which was in line with Experiment 1.

Discussion

Experiment 2 replicated the better recognition memory for low PE, i.e., memory congruency effect, and the absence of memory benefit for high PE which were found in Experiment 1. This stands in contrary to some previous studies (Brod et al., 2018; Greve et al., 2017; 2019; Kafkas & Montaldi, 2018; Quent et al., 2022) that documented better memory for events that elicit high PE. Despite not using pre-experimental knowledge to rule out the semantic memory processes and despite having a fully deterministic contingency in the prediction learning phase, better recognition memory results were obtained only for low PE. Notably, Experiments 1 and 2 both indicate coherently the lack of evidence for memory advantages for high PE.

General Discussion

Within two preregistered studies, we examined the effects of different PE levels on recognition memory performance. To test the hypothesized U-shape function of PE on episodic memory, we first asked our participants to learn novel contingency structures and generate predictions, then violated these predictions on three levels (i.e., low, medium, and high PE) with all levels being related to experimentally-induced prediction learning. We showed that participants were able to learn from the provided regularities and successfully formed predictions. Even though our findings indicated a strong verification for our manipulation of PE, there was no memory advantage for high PE level neither in the recognition nor in the association tasks. Rather, we consistently found a memory advantage for low PE trials, in line with memory congruency effect (Alba & Hasher, 1983; Anderson, 1981; Craik & Tulving, 1975). In addition to our primary findings, we exploratorily investigated the relationship between learning performance and recognition memory. We hypothesized that a better learning performance would lead to better recognition performance for high PE trials. Contrary to our hypothesis, the results were in line with our main findings suggesting a memory congruency effect but no memory advantage for high PE. Thus, the current studies clearly show that high PE does not guarantee subsequent memory benefit.

A body of research has shown that events giving rise to PE are remembered better, such that they facilitate new learning for better predictions in the future (Bein et al., 2021; Brod et al., 2018; Greve et al., 2017; Kafkas & Montaldi, 2018; Quent et al., 2022). Although PE is sometimes taken for granted as a driver of new learning (Greve et al., 2017), its direct behavioral effect on memory may depend on several factors, such as the task sensitivity concerning how PEs are experimentally generated and tested. One explanation why there was no memory benefit for high PE trials in the current studies can be the differences in the experimental paradigms, for example, how the encoding and the recognition phases were structured. In the following sections, we will discuss these points.

The first of these differences in the experimental designs can be examined via the differences in encoding of PEs. The studies which reported high PE benefits on memory had their PE manipulation and memory test based on the item level (Bein et al., 2021; Kim et al., 2017). In the current studies, we let our participants to generate predictions on the category level, because the task was to learn the associations between cue-target categories and predict the upcoming target category based on the cue. Nevertheless, participants were tested on their memory for the target (i.e., item level) at retrieval. Our participants might have only focused on the category-level information during encoding rather than on individual items which were tested later. Evidence for the effect of PE on association memory has also been demonstrated in previous studies (Greve et al., 2017; Quent et al., 2022). Unfortunately, the obtained association memory performance was below chance in our experiments. The difficulty level of study materials can be an issue both for musical instruments and the Wubbels. For example, participants might have found it challenging to discriminate guitar sounds from each other. On top of that, since processing the guitar sound category was already informative enough to accomplish the task, participants might have had a shallow encoding for the sounds.

Yet, another explanation for why the current studies did not show a memory advantage for high PE levels would stem from our experimental approach to assessing memory performance. Previous studies that provided a PE benefit tested recognition memory via alternative forced-choice tests (Greve et al., 2017; Quent et al., 2022) or mixed lists with similar lures (Bein et al., 2021; Frank et al., 2020), unlike our study which used an old/new paradigm. One can argue that PE creates distinct memory traces (i.e., snapshots) which leads to better recognition memory in return. However, it may not be possible to evaluate its memory traces via old/new paradigms since only a level of familiarity would be sufficient to dissociate the old items from the new ones. Even though we assessed the memory performance via confidence ratings to deal with the issue of familiarity, the results still did not suggest a memory benefit for high PE with high confidence.

On the contrary, our results were in line with the rich literature on the memory congruency effect (Alba & Hasher, 1983; Anderson, 1981; Craik & Tulving, 1975). One possible reason could be that high PE items were ignored because the task was making "better" predictions to correctly respond to what will be presented. During the encoding phase, participants were asked to predict the upcoming object category in their mind, and they were presented with objects with varying degrees of PE. In order to make correct predictions for the future, participants might have tended to leave out the items which were not in line with their predictions. This semantic encoding has been considered to have a great adaptive value to enhance the functionality of the memory system even though it may result in distortions (Schacter et al., 2011). For example, the previous research on the effects of confirmation bias on episodic memory suggests that participants tend to learn more from PEs that confirm their choices, indicating that events which are associated with successful decision-making are preferentially encoded (Palminteri & Lebreton, 2022; Pupillo et al., n.d.). In our study, the memory congruency effect can be interpreted as a byproduct of this processes that emphasizes the participants' responses which were later confirmed and utilized for future choices.

A recent framework, i.e., PACE (Gruber & Ranganath, 2019), postulated that enhanced memory encoding for PE is also based on the evaluation of information that can be valuable in the future. PEs might not be sufficient to trigger new learning because its appraisal is not important. As stated previously, high PE trials in our studies were not informative for the task at hand, potentially leading to these trials not being encoded better. One can thus infer that PE does not necessarily benefit memory. If events that give rise to PE are not evaluated as informative for future functioning, our memory system may tend to ignore them and rely more on the existing predictions.

Besides preceding explanations regarding why high PE does not benefit subsequent memory, additional evidence might derive from the research on cognitive conflict. A recent study (Ptok et al., 2021) showed that where the manipulation for conflict took place might have a crucial impact on the memory benefit. The authors run a series of experiments to investigate the effect of locus of processing conflict on memory benefit. They found memory benefit for incongruent items when the conflict is on the to-be-tested item. On the other hand, changing the attentional focus from the to-be-tested-item to the response does not lead to better memory. For example, Lisa (female name) with an incongruent distractor, male, would lead to a better recognition memory, whereas "Lisa – press right button" as an incongruent response information does not show a memory benefit. The authors concluded that having a violation and attentional focus on the to-be-tested item predicts the subsequent memory benefit. On the other hand, in our studies, although we had our PE (cf. conflict) on the individual level, namely the to-be-tested items, the task was to decide whether the presented object matched with participants' prediction. Therefore, participants might need to revisit their previous knowledge about the associations in order to do the task. As a consequence, they might have had an attentional switch from the item to the category level. This attentional switch could explain the better recognition memory for low PE trials than for high PE trials.

To conclude, our two preregistered studies provided novel paradigms to generate and violate PEs in varying degrees that indicated memory advantage for the events in line with predictions but not for the ones giving rise to PE. These findings suggest that it remains elusive to illustrate the U-shape relationship between prediction and memory. We conclude that it is important to investigate the specific condition in which a U-shape relationship could be reliably found. Relatedly, we showed in another study (Ortiz-Tudela et al., 2022) an inverted U-shape function instead of the U-shape function as suggested in the SLIMM Model (van Kesteren et al., 2012) in which we used a different experimental manipulation of continuous PE through prior strength. This indicated that the uncertainty level of generated prediction can modulate how PE affects memory. Our convergent results underscore that the effects of PE on episodic memory are complex, and there are potentially other modulating factors that may offer a better roadmap for further exploring PE as a driver of new learning and a possible reason for better memory.

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Author contributions: Author contributions are codded according to the CRediT taxonomy (Allen et al., 2014).
Gözem Turan: Conception, Methodology, Computation, Formal Analysis, Investigation – performed the experiments, Investigation – data collection, Data curation, Writing – writing the initial draft, Writing – review & editing, Writing – visualization, Project Administration
Isabelle Ehrlich: Conception, Methodology, Computation, Investigation – performed the experiments, Investigation – data collection, Resources, Data curation, Writing – review & editing, Project Administration
Yee Lee Shing: Conception, Methodology, Writing – review & editing, Supervision, Project Administration, Funding Acquisition
Sophie Nolden: Conception, Methodology, Writing – review & editing, Supervision, Project Administration, Funding Acquisition

Author notes: Data, scripts, and additional online materials are openly available at the project's Open Science Framework page (https://osf.io/pfgyb/). We have no conflicts of interest to disclose. The study was funded by a Starting Grant from the European Union for YLS (ERC-2018-StG-PIVOTAL-758898). The work of YLS was also supported by the German Research Foundation (Project-ID 327654276, SFB 1315, "Mechanisms and Disturbances in Memory Consolidation: From Synapses to Systems"), and the Hessisches Ministerium für Wissenschaft und Kunst (HMWK; project "The Adaptive Mind"). The work of SN was also supported by a Research grant Focus A/B, Goethe-University Frankfurt am Main, ("Dynamics of auditory and visual memory representations in the aging brain"). All authors approved the final version of the manuscript for submission. We would like to thank our student assistants Yi You Tan and Daniel Urban for their help with data collection.

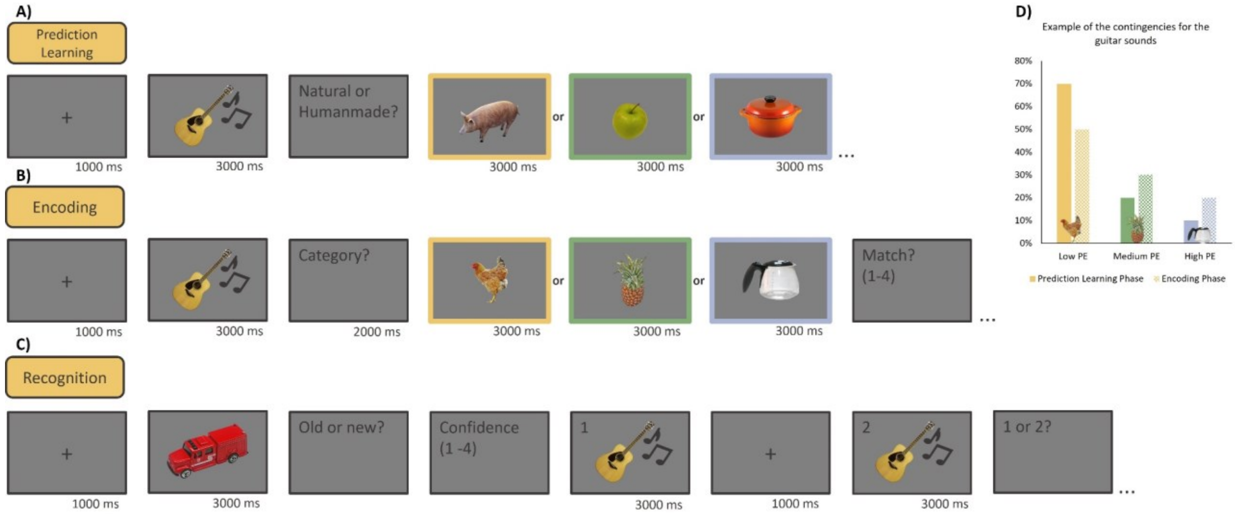

Figure 1. Study design for Experiment 1. The study was conducted on two consecutive days. A) On day 1, participants were asked to build up predictions about the sound-object category associations. In each trial of prediction learning phase, participants were presented with a musical instrument sound and asked to predict and indicate the upcoming object category based on two levels (i.e., natural and human-made). After their response, an object exemplar was shown. The contingency structure for the associations between sounds of musical instruments and object categories was unknown to participants. As also seen in panel D, the guitar sounds were followed by exemplar objects from animal categories 70% of the times (Low PE, yellow). Thus, the contingencies for exemplar objects from fruit categories (Medium PE, green) and human-made categories (High PE, blue) were 20% and 10%, respectively. B) On Day 2, during the encoding phase, a musical instrument sound was firstly presented. Participants were asked to predict the most likely object category in their mind among four different sub-categories. Participants were then presented with object pictures and asked to indicate if the presented object belongs to the same category they predicted. The contingency structure as follows, 50%, 30%, and 20% for low, medium, and high PE levels, respectively. C) During the recognition phase, participants were asked to make old/new judgments on the test pictures with their confidence ratings, and they were asked to indicate the paired sound as well. D) Example of the contingency structure for the guitar sound.

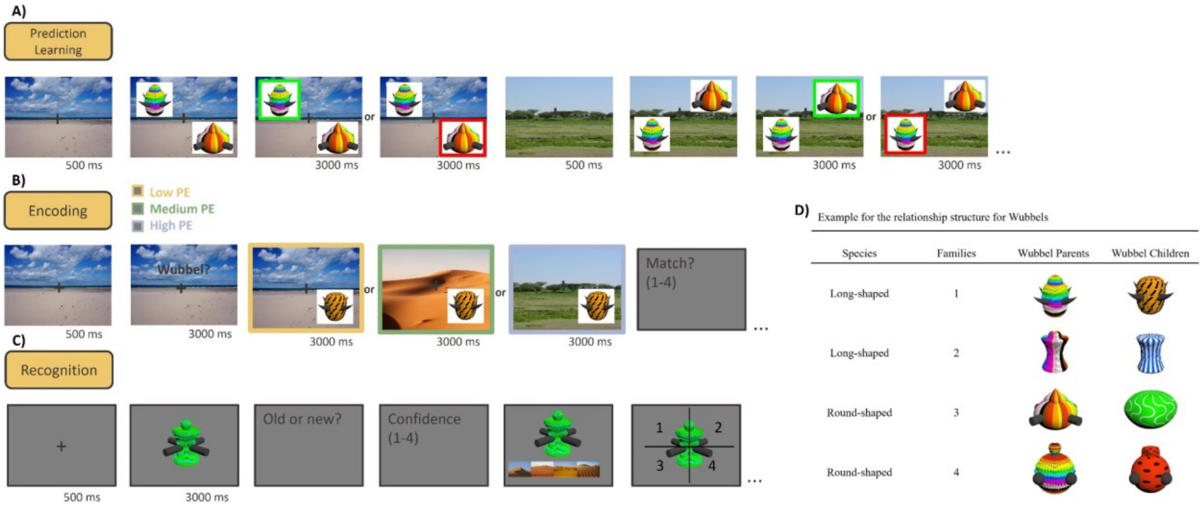

Figure 2. Study design for Experiment 2. The study was conducted on two consecutive days. A) On day 1, participants were asked to learn Wubbel family-environment category associations. In each trial of prediction learning phase, participants were presented with two Wubbel parents from different families on different screen locations and asked to indicate which Wubbel matches with the presented scene. Participants were then presented with feedback based on their response. As in the example, participants were expected to learn that one of the long-shaped Wubbel family lives on the beach. B) On day 2, the encoding phase was first run. Participants were presented with a scene and asked to predict the most likely Wubbel family in their minds. Then, a Wubbel child was presented on one out of four possible screen locations. Participants were further asked to indicate whether the presented Wubbel child belongs to the family which they predicted. As in the example, a long-shaped Wubbel child presented in a beach scene would elicit a low PE (yellow). Presenting the same Wubbel on a desert which was an environment for the other long-shaped family would lead a medium PE (green). Lastly, presenting the same Wubbel with the environments associated with the round-shaped families would elicit a high PE (blue). C) During the recognition phase, participants were asked to make old/new judgments and report their confidence. Participants were then asked to indicate the paired scene and paired location. D) Example for the relationship structure for Wubbel families and children.

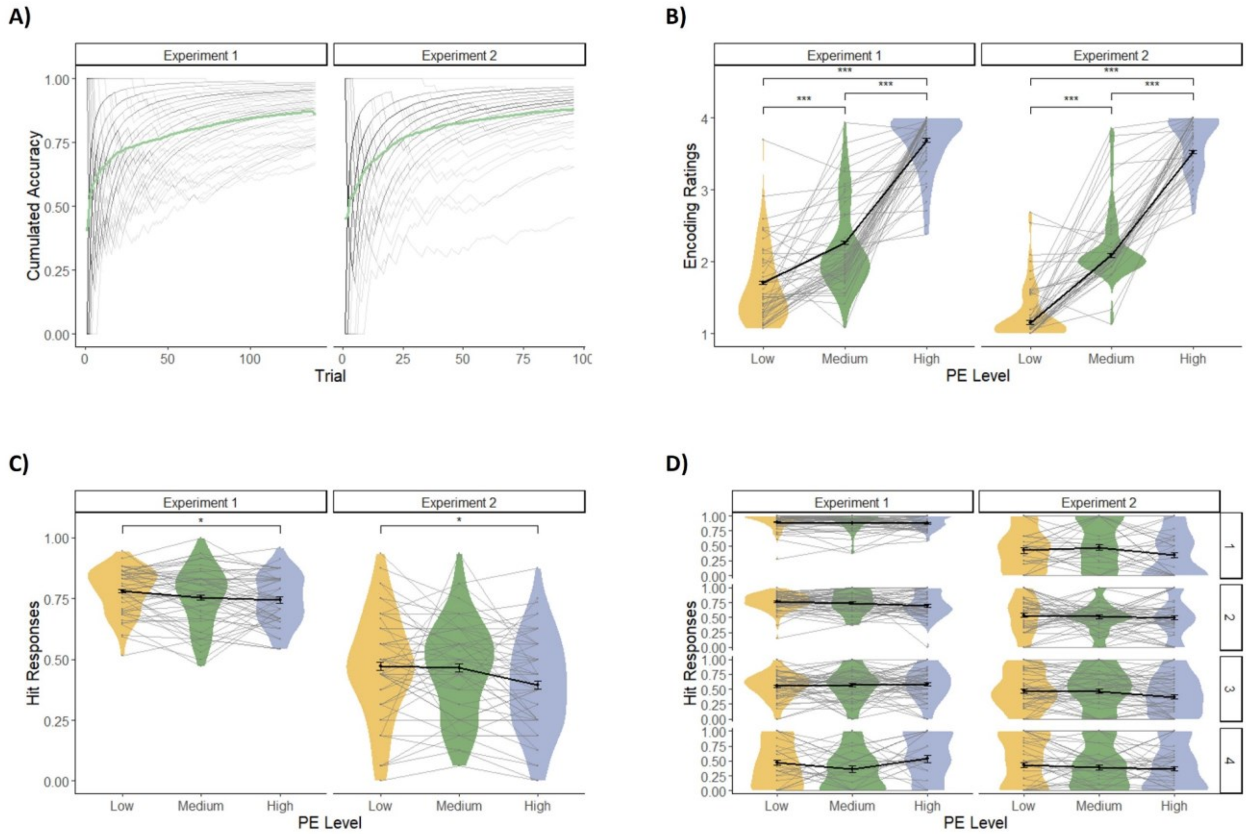

Figure 3. Results for Experiment 1 and 2. A) Cumulated accuracy for prediction learning. Grey lines indicate the performance of single participants. Green lines indicate the group mean. B) Encoding ratings for low, medium, and high PE levels. C) Hit responses for low, medium, and high PE levels. D) Hit responses for low, medium, and high PE levels separated by confidence ratings (1- Very sure, 2- Sure, 3- Unsure, 4- Very Unsure). Grey lines indicate the performance of single participants. Black lines indicate the group mean with error bars reflecting ± SEM. Asterisks denote statistically significant differences, * $p < .05$, *** $p < .001$

Original Manuscripts – Study 2

Unexpected Twists: Electrophysiological Correlates of Encoding and Retrieval of Events eliciting Prediction Error

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Data, scripts, and additional online materials are openly available at the project's Open Science Framework page (https://osf.io/sbc7d/). We have no conflicts of interest to disclose. The study was funded by a Starting Grant from the European Research Council for YLS (ERC-2018-StG-PIVOTAL-758898). The work of YLS was also supported by the German Research Foundation (Project-ID 327654276, SFB 1315, "Mechanisms and Disturbances in Memory Consolidation: From Synapses to Systems"), and the Hessisches Ministerium für Wissenschaft und Kunst (HMWK; project "The Adaptive Mind"). The work of SN was also supported by a Research grant Focus A/B, Goethe-University Frankfurt am Main, ("Dynamics of auditory and visual memory representations in the aging brain").

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Abstract

The human brain is postulated to function as a prediction machine, constantly comparing incoming sensory input to predictions based on past experiences. When an event contradicts these predictions, it results in a prediction error (PE), which has been shown to enhance subsequent memory. However, the neural mechanisms underlying the influence of PE on subsequent memory remain unclear. This study investigated the electrophysiological correlates during encoding and retrieval of events eliciting PE. We employed a statistical learning task in which participants were presented with pairs of objects in sequence. Subsequently, while recording electroencephalography (EEG), we introduced PE by replacing the second object of each pair with new objects and we then tested the participants' memory. Behaviorally, PE did not enhance memory. During retrieval, we observed higher amplitudes of the posterior recollection component for violation items that were remembered compared to those that were forgotten. In contrast, no evidence for the presence of the frontal negative familiarity component was found. These results suggest that recollection, but not familiarity, plays a crucial role in the interplay between PE and memory. Contrary to our hypothesis, we did not observe a relationship between PE and the P3 component during encoding. In conclusion, our study contributes to the growing body of knowledge concerning the intricate relationship between PE and episodic memory. It sheds light on the underlying neural mechanisms involved and emphasizes the importance of recollection in this context.

Keywords: prediction error, statistical learning, episodic memory, predictive processing, Electroencephalography, Event-Related Potentials

Introduction

Although the first season of Game of Thrones was broadcast 12 years ago, many viewers still remember the execution of the main character, Ned Stark. According to storytelling conventions, the viewers of the show might have predicted that the protagonist would ultimately be spared or that justice would be served in the end. However, when Ned was beheaded in a sudden twist, it violated the viewers' prediction. This violation might have led the viewers to process the unexpected event in a distinctive way since it differed from their prediction. Distinctive processing could explain why Ned's execution remains such a memorable event, illustrating the role of prediction error (PE) in memory processes. Indeed, whether and how PEs modulate memory is a topic of intense investigation in cognitive psychology and neuroscience (Aitchison & Lengyel, 2017; Ergo et al., 2020; Quent et al., 2021). Here, we investigated the electrophysiological correlates of encoding and retrieval of PE to gain a better understanding of the relationship between PE and memory.

According to the predictive processing framework, our brain constantly predicts likely occurrences based on past experiences (Bar, 2007; Friston, 2010; Henson & Gagnepain, 2010). The brain continually compares sensory information with its predictions. When a prediction is confirmed, it reinforces existing internal models and increases confidence in future predictions. Conversely, when a prediction is violated, a PE occurs, signaling the need for additional processing to update predictions. This way, the brain utilizes PE to adaptively refine its predictions over time. However, we have limited knowledge regarding how the brain processes events that give rise to PE and how the underlying mechanisms contribute to subsequent memory.

Previous research showed that PE facilitates memory. These studies have suggested that events accompanied by PE contain significant information that requires enhanced encoding for memory (Bein et al., 2021; Brod et al., 2018; Kafkas & Montaldi, 2018; Quent et al., 2022). Improved encoding of events that elicit PE might generate detailed 'snapshots' of these events, resulting in a memory advantage (Henson & Gagnepain, 2010). Additionally, PEs might enhance pattern separation, a process by which distinct memory traces are created, potentially separate from those associated with previous predictions (Frank et al., 2020). Furthermore, according to event segmentation theory (Zacks et al., 2007), which addresses how continuous experience is separated into discrete events, PE triggers an upregulation of attentional resources toward the specific event. This increased attention enables the brain to process information more deeply and prompts the identification of an event boundary, potentially leading to the separation of events and to robust memory. Triggering an event boundary in this manner aids in segmenting the continuous stream of sensory information into discrete events and facilitates subsequent memory benefits (Wahlheim et al., 2022). To summarize, previous research suggests that events giving rise to PE are encoded more effectively and result in better memory.

In addition to encoding, retrieval processes might also contribute to how PE enhances memory. For example, a recent study by Kafkas and Montaldi (2018) investigated the effects of PE during encoding and retrieval. Their results revealed that predicted events enhanced familiarity, which refers to a subjective feeling that an event has been experienced before, while unpredicted events enhanced recollection which involves the retrieval of specific episodic details (Cowell et al., 2019). This finding aligns with the framework proposed by Henson and Gagnepain (2010), which suggests that predictive events aided by familiarity benefited during the retrieval. Conversely, unpredicted events elicit a memory characterized by snapshot-like details, leading to enhanced recollection. A relevant concept is the selective retrieval process (Lu et al., 2022), which proposes that error signals originating from PE may contribute to subsequent recollection during retrieval (Fenerci & Sheldon, 2022; Wahlheim et al., 2022). Taken together, these findings suggest that the effects of PE on memory are not limited to the encoding stage but also extended to retrieval phase.

Notwithstanding the importance of the aforementioned studies, PEs might not always enhance memory. A recent body of research has consistently reported that PE does not guarantee subsequent memory advantage (Nolden et al., 2023; Ortiz-Tudela et al., 2023; Turan et al., 2023). For instance, in one study, participants were asked to make explicit predictions regarding associations between sequentially presented pairs, and these predictions were either met or violated in varying levels of PE. The results revealed better recognition memory for items that were consistent with participants' predictions but not for items eliciting PE. These results are consistent with prior work showing better memory for expected compared to unexpected events, indicating a memory congruency effect (Alba & Hasher, 1983; Brod & Shing, 2019; Craik & Tulving, 1975; Liu et al., 2018; Ortiz-Tudela et al., 2017). Thus, the effect of PE on subsequent memory is not straightforward and further exploration is warranted. Currently, there is limited empirical evidence regarding the reliable conditions under which PE facilitates memory, highlighting the need for additional research.

Through the investigation of how the brain processes PE and how its underlying operations influence subsequent memory, we can enhance our understanding of the effects of PE and potentially reconcile the divergent findings in the literature. Event-related potentials (ERPs) can provide an ongoing evaluation of neural processes that correlate with PE. By comparing the time-locked changes in the brain's electrophysiological activity in response to violating events that are later remembered versus later forgotten, we can identify neural processes that contribute to subsequent memory enhancement for PE. For instance, the P3 component has been one of the highly studied ERP components which was traditionally associated with oddball signals (Polich, 2007), attention (Kramer et al., 1985), evaluation of novelty (Friedman et al., 2001), and context updating (Donchin, 1981). It has also been demonstrated that P3 amplitude is an indicator of successful subsequent memory (Fabiani et al., 1986). This implies that memory-related changes in P3 amplitude might index encoding processes that might accompany PE (even if not specific to PE) and that facilitate subsequent memory. Furthermore, in addition to the mentioned traditional origins, P3 has also been linked to reward PE (see a recent meta-analysis, Stewardson & Sambrook, 2020), novelty processing influenced by expectations (Schomaker & Meeter, 2018) and hierarchical violations as suggested by the predictive coding theory (Vidal-Gran et al., 2020). Even though these studies demonstrated the associations between P3 and the processing of violation (i.e., PE), it is still unclear whether P3 elicited by violations contributes to the subsequent memory of events that violate these predictions.

At the retrieval side, behavioral and neural research suggests two distinct processes that contribute to memory recognition: familiarity and recollection (Jacoby, 1991; Mandler, 1980; Yonelinas, 2002; see a recent review Cowell et al., 2019). As previously defined, recollection involves the assessment of specific details of an episode. Familiarity, in contrast, is the subjective feeling that an event has been experienced before, but in the absence of additional mnemonic details. ERP studies have indicated that recollection-based memory is associated with a parietal effect occurring between 400 and 800 ms, while the familiarity effect is observed between 300 and 500 ms in frontal sites (Curran & Cleary, 2003). As previously mentioned, behaviorally, the effects of PE on memory have been shown to extend to the retrieval phase, with distinct differences between behavioral measures of familiarity and recollection (Kafkas & Montaldi, 2018). However, neural evidence underlying these differences is thus far lacking.

To gain a deeper understanding of how PE influences the encoding and retrieval processes and their impact on episodic memory, we investigated the relationship between PE, its ERP components, and memory within a single paradigm. We employed a statistical learning paradigm, whereby participants implicitly learned sequentially presented object pairs embedded within a stream of objects over two consecutive days (Bein et al., 2021). On the third day, new objects were introduced into the list. Half of the new objects were inserted instead of the second item of the pair, inducing PEs (violation items). The other half was presented between pairs, serving as a non-violation baseline. Subsequently, participants' memory was assessed. We recorded electroencephalography (EEG) during encoding and retrieval phases.

We expected to replicate previous behavioral findings (Bein et al., 2021), which demonstrated better memory performance for events that elicit PE compared to events that did not violate predictions. Additionally, we hypothesized that violating events that were later remembered would elicit larger P3 amplitudes compared to violating events that were later forgotten. Inspired by previous behavioral research (Kafkas & Montaldi, 2018), we hypothesized that during retrieval, recollection effects would be observed in ERPs for previously violated trials that were remembered, while familiarity effects would be observed in ERPs for non-violation trials that were remembered.

Method

Participants

51 university students (32 women, 13 men, mean age 23.52 (*SD* = 2.67)) were recruited for the study. A target sample size of 40 participants was determined by a power analysis of generalized linear mixed models (Green & Macleod, 2016) on our pilot data from 13 participants, which was not part of the final sample. The model was calculated with maximum-likelihood estimation and participants as random intercept to account for between-participant variability in the P3 mean amplitude during the violation phase. As fixed factors, we included the within-participant factor of condition (violation and non-violation) and item recognition accuracy (later remembered and later forgotten). The effect size for the interaction

between condition and item recognition accuracy obtained from the pilot participants was .28. We accounted for potential effect size inflation by taking 90 % of the effect size. Thus, we aimed to detect an effect size of .25 with the standard .05 alpha error to obtain 80 % power. The pilot data and analysis scripts can be found at the study's OSF page (https://osf.io/sbc7d/).

Participants were recruited through an online experiment scheduling system of Goethe-University Frankfurt am Main and personal contacts. All participants reported normal or corrected-to-normal vision, no neurological or psychiatric disorders, and right-handedness. They were asked to sign informed consent approved by the local ethics committee of the Goethe-University Frankfurt prior to the study, debriefed at the end, and compensated either with 10 € per hour or partial course credits.

Since the primary objective of the study was to examine the effects of violation on memory performance, we set two main exclusion criteria to ensure clear interpretation of the results. In accordance with our pre-registered plan, we excluded six participants with poor associative memory performance of less than 40 % accuracy rate and who showed poor recognition memory performance, meaning d' below .35. Additionally, four participants due to missing or noisy EEG data were excluded from the further analysis steps. We ran the statistical analysis on the remaining 35 participants (26 women and 9 men, mean age 23.26, *SD* =3.24).

Material

The stimulus set consisted of 370 pictures of everyday namable objects from the database used in the previous study (Bein, et al., 2021). The set was altered only in a few instances, where a picture of an object that may not be common in Germany was replaced with another object picture. The objects were presented with a white square background sized set to 350 x 350 pixels. The images were equally divided into two main categories according to their real-life size based on whether they are bigger than a shoe box or not.

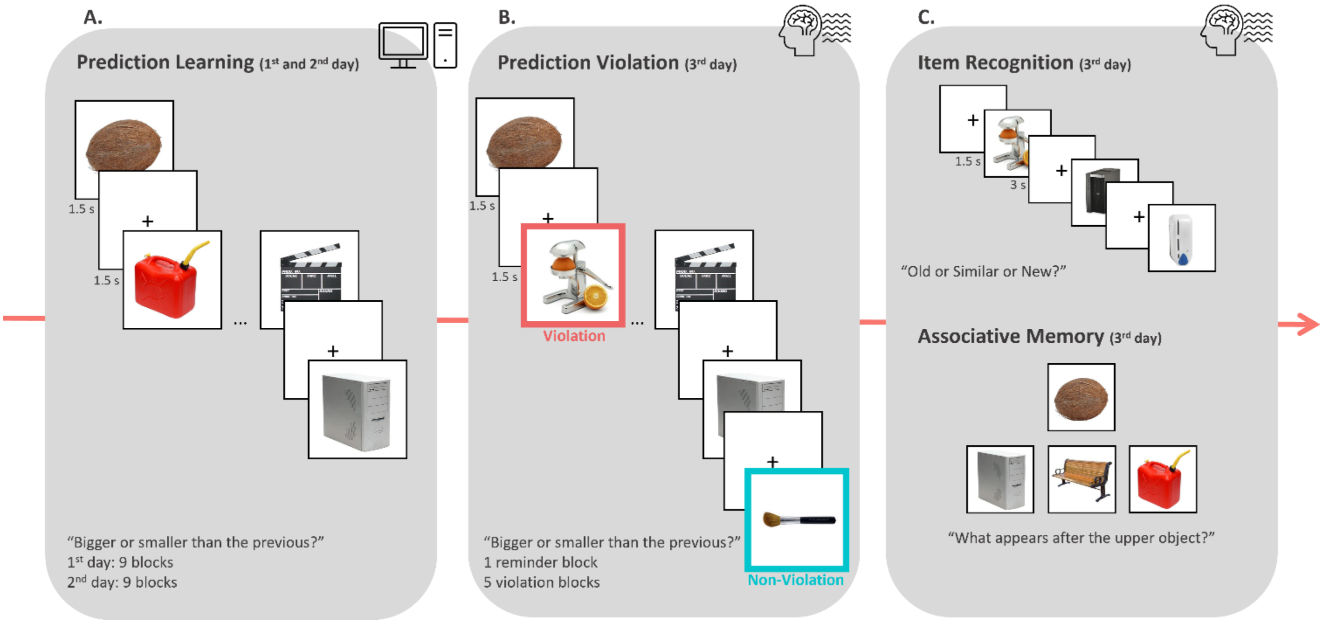
General Procedure

The study was conducted over three consecutive days (Figure 1). On the first two days, prediction learning phase took place and violation and retrieval phases were employed on the third day. Participants were presented with object pictures and asked to indicate if the presented object was bigger or smaller than the previous one. However, unbeknownst to the participants, there were pairs of objects that always followed each other, while the order of the pairs was randomized in each block. Participants who did not demonstrate signs of learning the pairs during the statistical learning phase were not invited to the third session, as they would not engage in prediction violation phase and therefore not experience PE. Thus, based on participants' response times (RTs) and accuracy rates on the bigger and smaller task, we decided if they were eligible to participate in the third day. We invited participants with RT differences of less than 200 ms between the first and second items across pairs and with accuracy rate more than 90 % (n = 45). The third day started with a reminder, which included one block identical to the learning phase. Then, during the prediction violation phase, half of the original pairs were violated by replacing the second item in the pair with a new item. The other half remained intact and were followed by a new item to create a non-violation baseline. Participants were then tested on surprise item recognition memory and associative memory, with a distraction task before and after the recognition memory phase.

To ensure participants' comfort and attention, we divided each task into multiple blocks and advised taking breaks in between. All instructions were provided both verbally and in written form. We used PsychoPy v2021.1.4 (Peirce, 2007) to program the stimulus presentation and response collection. Each session was scheduled approximately 24 hours apart.

Figure 1

Study Design



Note. A. During prediction learning (Day 1 and 2), participants viewed pairs of sequentially presented objects and asked to indicate whether each object was bigger or smaller than the previous object. B. In the prediction violation phase (Day 3), new object pictures were inserted into the sequence of objects, either instead of the second object in the pair (violation) or after the second object in a pair (non-violation). C. Following the violation phase, participants completed an item recognition memory test (Day 3) where they were presented with violation and non-violation targets, similar lures, or new items, and were asked to indicate whether each item was old, similar, or new. Memory for the original predictive pair was also tested (associative memory) by presenting participants with the first object in a pair and asking which of three objects followed the top object.

Prediction Learning Phase

The prediction learning phase used a statistical learning paradigm to build-up predictions about object pairs. Participants implicitly learned sequentially presented object pairs embedded within a stream of objects over two consecutive days (Kim et al., 2017; Schapiro et al., 2012; Turk-Browne et al., 2012). Unbeknownst to the participants, there were object pairs that always followed each other, while the order of the pairs was randomized in each block. Each pair consisted of a big and a small object. Half of the pairs were presented with the big object first and the other half with the small object first. The pairing of objects was randomized for each participant while ensuring that each pair included one big and one small object.

During the task, participants were presented with a stream of object pictures and asked to indicate if the presented object was bigger or smaller than the previous one. Each trial started with a fixation cross at the center of the screen for 1.5 seconds and was followed by the object picture for 1.5 seconds. Participants were then asked to give a response by pressing C or M keys on the keyboard with their left or right index fingers. They were instructed to be as fast and as accurate as possible. Despite all object pictures on the screen appearing to be relatively the same size, they should base their judgments on the real-life sizes of the objects. Before the initial task, participants received detailed instructions and completed eight practice trials. For each day, all participants completed 200 trails (100 pairs) equally spread over nine blocks.

Reminder Phase

The third session of the study took place in the EEG laboratory. It started with a reminder phase, which was constructed as a block of the prediction learning phase. Participants covered one block of the previously presented 100 original pairs, in total 200 trials.

Prediction Violation Phase

Immediately after the reminder phase, participants were presented with the prediction violation phase. The task structure was the same as the previous phases (i.e., prediction learning and reminder phases) and participants were not provided with additional instructions. Therefore, they were not explicitly informed of the transition to the prediction violation phase. In order to violate the pair associations, we added new object pictures to the list. For the violation condition, half of the original pairs (i.e., 50) were violated by replacing the second item in the pair with a new object picture. The other half of the original pairs (i.e., 50) remained intact and were followed by a new object picture to generate the non-violation condition as a baseline. Only the identity of the item was violated but not the response, meaning that we replaced previously presented small objects with small new object pictures, and likewise big object pictures. Within each block, all pairs were presented twice. First, the original pairs were presented. For the second presentation, half of the pairs were violated, while the other half remained intact. There were 20 original pairs in each block. The presentation of the original, violation, and non-violation pairs were randomized, with the constraint that there were at least six pairs between an original pair and its subsequent appearance as a violation or non-violation pair. The prediction violation phase consisted of five blocks of 90 trials, for a total of 450 trials.

Distraction Phase

Before and after the Item Recognition Phase (see below), participants performed a distraction task for three minutes in which simple math equations were presented together with three alternative forced choices. In each trial, an equation was presented in the center of the screen and three response options appeared below. Participants used the “A”, “S”, or “D” keys on the keyboard to select the correct response and responded with their left hand's ring, middle, or index finger. The respective letters were displayed under the response options to indicate the response keys. Once participants responded, the equation disappeared, and a new one appeared after a 500 ms delay. We informed participants to be as fast and accurate as possible.

Item Recognition Phase

To test item recognition memory for both violation and non-violation items, participants were presented with object pictures and were asked to indicate if the presented object was old, similar, or new. A total of 170 items were presented with 80 being identical to the items presented during the violation phase (half of the items were violation items and the other half was non-violation items), 20 being similar lures that were different exemplars of objects presented during the violation phase, 20 being similar lures to the objects just seen in the recognition phase. In addition to violation items, non-violation items, and similar lures, 50 new object pictures were also included. Our main focus was on the old trials. For that reason, we added similar lures to execute the task, while maximizing the number of old trials we could use for analysis.

Each trial started with a fixation cross at the center of the screen for 1.5 seconds and was followed by the object picture for three seconds. To give a response, participants were instructed to press left, right, or down arrow keys on the keyboard with their ring, middle, or index finger of the right hand. The mapping of the left and right arrow key to indicate “old” or “new” responses was counterbalanced, while the down arrow key was consistently used for “similar” responses. Participants were clearly instructed to respond with “old” if the object was the same as an object presented during the previous phase, “similar” if the object was presented before, but it was not the exact object in the previous phase (i.e., a different exemplar), and “new” if the object was not presented before. During the task, there were indicators to provide participants to show which key to use for each response which disappeared once response was made. They started with a practice phase consisting of 12 trials via detailed instructions from the experimenter. All participants completed 85 trails equally spread over two blocks.

Associative Memory Phase

After the item recognition phase, participants were given the second distraction task to reduce potential interference between the two memory phases. This was followed by an associative memory test, in which we aimed to assess explicit memory of the original pairs which were studied during the first two sessions of the study (i.e., prediction learning phase). At the beginning of each trial, a fixation cross appeared at the upper center of the screen for 1.5 seconds. The first item of a pair was then presented at the upper center of the screen, accompanied by three alternative items located at the lower part of the screen. One of the three alternatives was the second item that corresponded to the first item of the original pair (i.e., target item). The other two alternatives were chosen from the second items that belonged to the same size category as the target item. Participants were asked to indicate which object appears after the upper object by pressing “A”, “S”, or “D” keys on the keyboard with their left hand's ring, middle, or index finger. Indicators were presented during the task to guide participants on which key to press for each object response. These indicators disappeared once the participant had made a response. 100 trials were tested in one block after a practice phase of eight trials.

EEG Recording and Preprocessing

EEG was recorded during the third day of the study with 64 Ag/AgCI BrainProducts active electrodes (actiCAP; Brainproducts, Munich, Germany) following the international 10–10 system at Fp1, Fpz, Fp2, AF7, AF3, AF4, AF8, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FT7, FC3, FC1, FC2, FC4, FT8, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, PO9, P7, P5, P3, P1, Pz, P2, P4, P6, P8, PO10, PO7, PO3, POz, PO4, PO8, O1, Oz, and O2 electrodes with a sampling rate of 1000 Hz (actiCHamp Plus amplifier; Brainproducts, Munich, Germany), online band-pass filtered between 0 to 100 Hz. EEG data were online referenced to the left mastoid and a common ground was placed at the FCz. To record eye movements, three additional electrodes were placed at the outer canthi (horizontal electrooculography, EOG) and below the left eye (vertical EOG). Electrode impedance values were maintained below 20 kΩ during the recording.

EEG data preprocessing were performed offline with custom scripts in MNE-Python (Gramfort et al., 2014). It was run for each participant separately. As the first step, data were re-referenced to both mastoid electrodes. Then, an independent component analysis was applied to correct eye blinks on cropped and high pass (i.e., 1 Hz) filtered data. Those components were corrected in three steps: automatic detection, visual check, and correction.

Hereafter, data epochs were extracted according to the stimulus-locked experimental conditions 100 ms prior to the onset of the stimuli presentation through 1500 ms post-stimuli. We excluded the epochs containing values higher than 60 µV. The Autoreject function (Jas et al., 2017) was used to detect, interpolate, and reject bad epochs. Lastly, baseline corrected data were filtered between 0.1 and 30 Hz. After preprocessing, the mean total number of violation trials was 47.49 (*SD* = 2.89) and non-violation trials was 47.83 (*SD* = 2.37) during the violation phase. For the recognition phase, the mean total number of violation trials was 38.31 (*SD* = 2.30) and non-violation trials was 37.94 (*SD* = 2.48).

Behavioral Analyses

As the first step, we calculated participants' "old" response rates to violation and non-violation items, following Bein et al. (2021) to compare our results. This was done only for the items for which the original pair was remembered correctly in the associative memory task. Second, we calculated classification indices based on confusion matrices (Ngo et al., 2020) to capture mnemonic discrimination. These classification indices are more sensitive than the traditional signal detection measures such as d' and receiver operating characteristic curves (see also Nolden et al., 2023). To calculate classification indices, we first calculated the precision and sensitivity of violation and non-violation items, each separately. Precision was computed as the ratio of correct old responses to all old responses, while sensitivity was calculated as the ratio of correct old responses to all old items. A classification index was then determined by multiplying precision and sensitivity by two, adding them together, and then dividing by the sum of precision and sensitivity (Ngo et al., 2020).

We then conducted general linear mixed-effect models for response rates and linear mixed-effect models for classification indices to investigate whether violation was a significant predictor of memory performance. The models included participants as random intercepts, violation as fixed effect and random slope. Starting from the full model, we compared the explanatory power of each model for the random effects via likelihood ratio test. We reduced the fixed effects by removing non-significant predictors and interactions, and then compared these reduced models. Maximum likelihood ratio was assessed for model estimations and $\chi2$ (chi-squared) was used for the statistical significance of the fixed effects. The model comparisons repeated until a significant decrease was observed. We also compared the models using AIC (Akaike Information Criterion) and BIC (Bayesian Information Criterion). An analysis of variance (ANOVA) was conducted to compare models in terms of their model fit and determine if the inclusion of random slopes for violation condition significantly improved model. In the case of a significant interaction effect, we used the emmeans function to calculate estimated marginal means and performed post hoc tests with Bonferroni adjustment to compare the levels of predictors for each level of the other variable. All analyses were conducted with custom-made R scripts (lme4 package: Bates et al., 2015) and can be found on the study's OSF page (https://osf.io/sbc7d/).

ERP Analyses

To investigate electrophysiological correlates of PE, we measured P3 mean amplitude values at parietal electrodes during the violation phase. The mean amplitude values were calculated for the familiarity and recollection components during the item recognition phase. ERPs were time-locked to the onset of the stimuli. In line with our pre-registered report, we defined time windows and electrodes for each component differently. The time window for the P3 component was 400 – 800 ms at centroparietal electrodes (CP3, CP1, CPz, CP2, CP4, P3, P1, Pz, P2, and P4). The familiarity component was obtained during 300 – 500 ms after stimulus onset at frontocentral (F3, F1, Fz, F2, F4, F3, FC1, FC2, and FC4) electrodes. Lastly, the recollection component was measured from 400 to 800 ms at parietooccipital (P3, P1, Pz, P2, P4, PO3, POz, and PO4) electrodes.

As suggested by Frömer et al. (2018), linear mixed effect models were used to analyze trial-based data with lmer function (lme4 package: Bates et al., 2015). The participants' mean-centered amplitude values were introduced as fixed effects and modeled separately for P3, familiarity, and recollection components. Participants and objects were added as random intercepts. The random slopes were modeled for the predictors: violation condition (violation vs. non-violation) and item accuracy (remembered vs. forgotten). As in the behavioral analyses, we follow the same rationale to test model comparisons for the random and interaction effects.

We also exploratorily used spatiotemporal cluster-based permutation t-tests (CBPT) to check the time window and topographical distributions. We created 3D data with channels, time points, and trials by participants for all scalp electrodes. Clusters were created by grouping adjacent channels and time points where the *p*-values were lower than .05. The sum of all *t*-values within a cluster was used to detect the following test statistic. This involved randomly assigning the samples into two classes and contrasting the differences between these random classes with the actual differences between our experimental conditions (e.g., violation vs non-violation trials for the prediction violation phase). This process was repeated 10,000 times for each permutation. Later, *t*-statistics were calculated for each permutation and *t*-values were summed for each cluster. Lastly, we tested clusters with *p*-values lower than .05 with an additional linear mixed model as suggested by Sassenhagen and Draschkow (2019)[7]. All analyses were run with custom MNE-Python scripts (Gramfort et al., 2014) and can be found on the study's OSF page (https://osf.io/sbc7d/).

Results

[7] In their simulation study, Sassenhagen and Draschkow (2019) showed that discovering a cluster does not guarantee that the experimental conditions within that cluster differ significantly from each other. Therefore, it is important to conduct additional analyses to further investigate the statistical differences between experimental conditions.

Behavioral Results

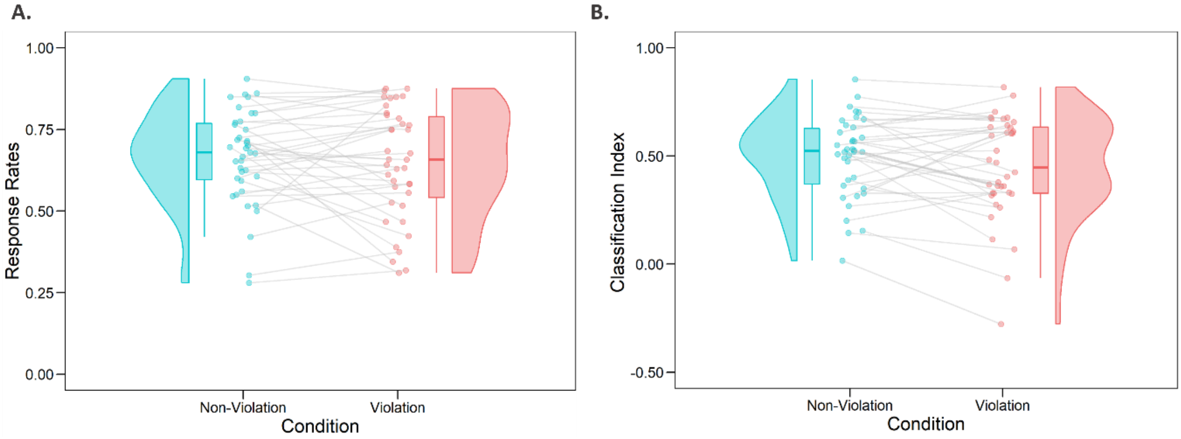
Before conducting our primary analysis on the response rates and classification index, we first checked if participants learned the object pairs to build up predictions. Thus, we investigated the results from prediction learning, reminder, and associative memory phases. The RTs during the prediction learning and reminder phase were faster for the second item of the pair (M = .56, SD = .10) than the first pair (M = .72, SD = .15), $t(1, 38) = 60.97$, $p < .001$, d = .38, indicating a learning process due to prediction of the upcoming object (see Appendix A.). The accuracy rate during the associative memory phase to test original pairs was .78 (SD = .17) and all participants selected the associated pair significantly above chance level, $t(38) = 39.20$, $p < .001$, d = 4.44. The accuracy rate for the original pairs was not different between violation and non-violation trials, $t(38) = -.01$, $p = .99$.

For the effects of PE on item recognition memory performance, the response rates and classification index are displayed in Figure 2. First, the full model to test the effect of violation condition on response rates did not show a significant main effect, $\chi^2(1) = .39$, $p = .53$, and the full model did not significantly differ at the reduced model without violation as a predictor, $\Delta\chi^2(2) = 3.39$, $p = .18$. Secondly, the classification index did not differ between violation items (M = .45, SD = .24) and non-violation items (M = .49, SD = .19), $\chi^2(1) = 3.50$, $p = .06$. All together, these findings indicate that there was no significant difference in item recognition memory performance between violation and non-violation trials[8]. Although we did not find a behavioral difference in response rates and classification index, we proceeded to investigate our main hypotheses concerning ERP components as they could give better insights into mechanisms involved in encoding and retrieval processes of PE.

Figure 2

[8] In addition to response rates and classification index, we also calculated d' scores as stated in the pre-registered report. The results did not show a main effect of violation on d' scores, either, $\chi^2(1) = 2.37$, $p = .12$.

Response Rates and Classification Index



Note. The raincloud plot shows the distribution of response rates and classification index for violation and non-violation conditions. A. Proportion of old responses to old items. B. The proportion of correct responses (true positives and true negatives) out of all instances. The box plots display the median, interquartile range, and 95 % confidence interval for each group using, while the density plots show the distribution of the data points for each condition. The individual data points are displayed as scatter plots.

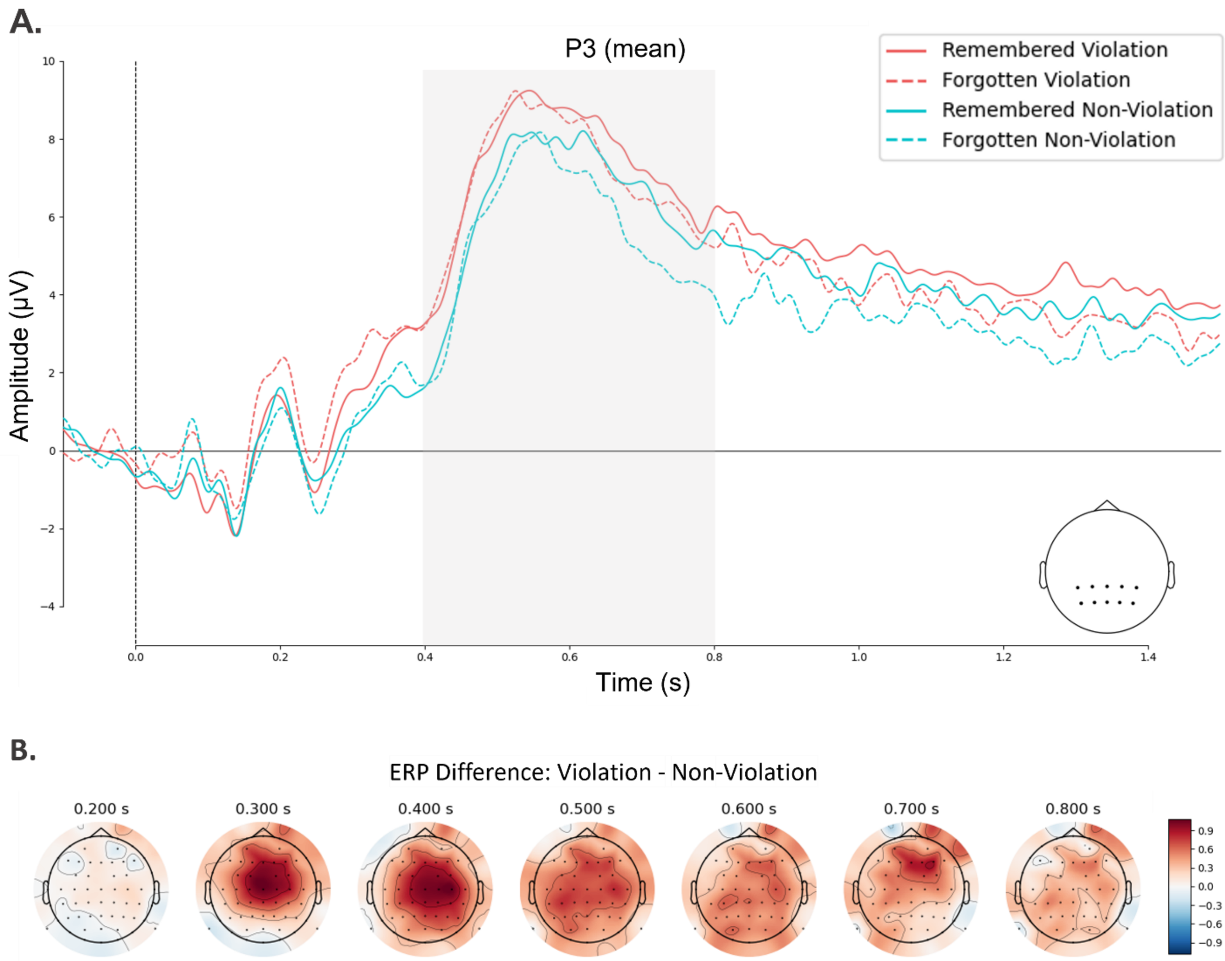
ERP Results

P3 Amplitude During Encoding

The ERP results for the P3 amplitude can be seen in Figure 3. The average mean amplitude values are displayed in Figure 4A. We ran the analysis with mean amplitude values measured at centroparietal electrodes within the time window of 400 ms and 800 as in the pre-registered report. We started with the full model with participants and objects as random intercepts and random slopes together with random slopes for the predictors to examine how P3 amplitude is influenced by violation condition and item accuracy. Model comparison favored the reduced model excluding violation, item accuracy, and their interaction as random slopes, $\Delta\chi^2(18) = 8.05$, $p = .98$ (AIC: 23394 vs 23366, BIC: 235451 vs 23408). The reduced model showed that the main effect of violation condition ($\chi^2(1) = 2.59$, $p = .11$), item accuracy ($\chi^2(1) = 3.24$, $p = .07$), and the interaction effect ($\chi^2(1) = .08$, $p = .08$) was not significant. CBPT to compare violation and non-violation trials found a cluster from 260 ms after stimulus onset to 532 ms for 53 electrodes (see Appendix B.). Converging with the fixed time-window analysis above, the results did not show a significant main effect of condition on mean amplitude values, $\chi^2(1) = 1.65$, $p = .21$.

Figure 3

P3 component during the violation phase



Note. Stimulus-locked ERPs during the prediction violation phase. A. Color-coded ERP grand average recorded at centroparietal electrodes with highlighted time window in gray. B. Topographical map plot of violation minus non-violation difference in the P3 time window.

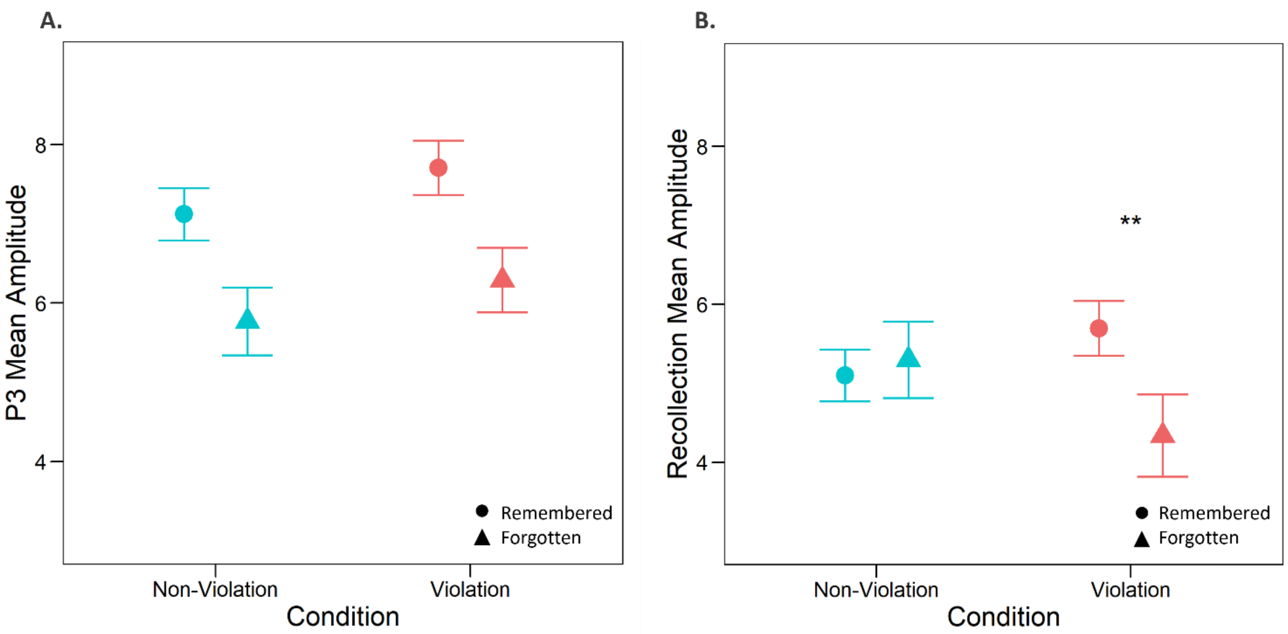
Recollection Component Amplitude During Retrieval

Figure 5 displays the ERP outcomes for the recollection component. Figure 4B shows the average mean amplitude values for each condition. We conducted an analysis using mean amplitude values obtained at parietooccipital electrodes between 400 and 800 ms, as pre-registered. To test the effects of violation condition and item accuracy on the recollection component amplitude, we run the full model with participants and trials as random intercepts and random slopes together with random slopes for the predictors. Model comparison favored the reduced model excluding violation, item accuracy, and their interaction as random slopes,

$\Delta\chi^2(18) = 12$, $p = .81$ (AIC: 18445 vs 18421, BIC: 18591 vs 18462). In this reduced model without random slopes, the main effect of violation condition ($\chi^2(1) = .02$, $p = .88$) and the item accuracy ($\chi^2(1) = 2.55$, $p = .11$) was not significant. However the interaction of violation and item accuracy was significant, $\chi^2(1) = 3.87$, $p < .05$. The follow-up results showed that remembered violation trials had higher amplitudes than forgotten violation trials, $b = 1.31$, $SE = .52$, $p = .01$. There was no significant difference between remembered non-violation and forgotten non-violation trials, $b = .15$, $SE = .54$, $p = .78$.

Figure 4

Average ERP amplitude values

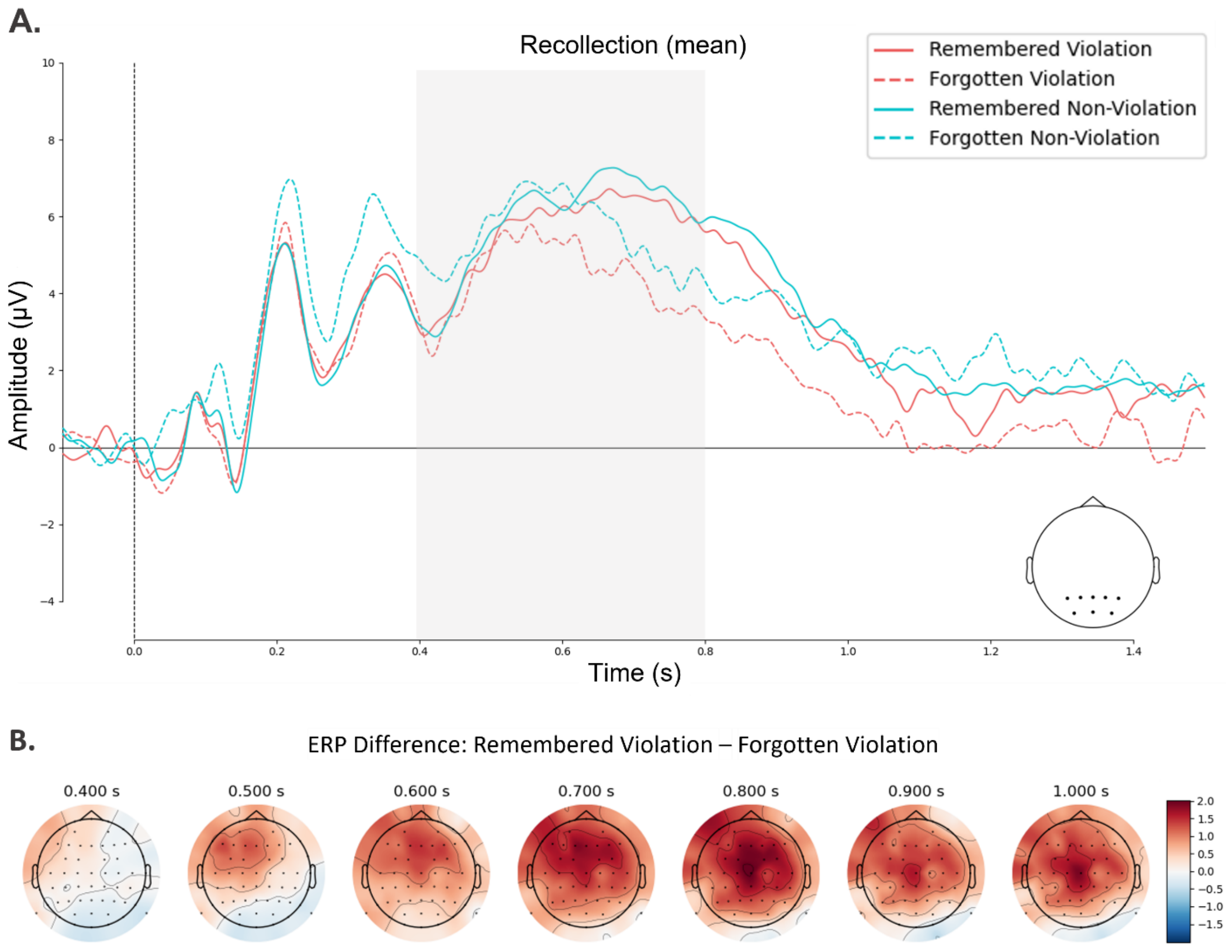


Note. Average ERP amplitude values for each condition within the relevant time windows. Error bars represent the within-participant standard error of the mean. A. Mean amplitude values of P3 component during the violation phase. B. Mean amplitude values of recollection component during the item recognition phase. ** $p < .01$.

Since we hypothesized that amplitude values during the late window of the item recognition phase would be higher for remembered violation items compared to forgotten violation items, suggesting a recollection effect, we conducted a CBPT only for remembered versus forgotten violation items. The results revealed a cluster between 524 ms and 1.177 ms after stimulus onset, involving 56 electrodes (see Appendix C.). There was a significant main effect of memory performance on mean amplitude values, $\chi^2(1) = 8.38$, $p = .01$, namely there was higher amplitude values for remembered violation than forgotten violation trials (b = 3.25, SE = .80, $p < .001$). Additionally, we run a CBPT only for non-violation trials to test the effect of item memory, which found a cluster between 625 – 869 ms (see Appendix D). Yet, the main effect of memory performance on mean amplitude values was not significant, $\chi^2(1)$ = .31, $p = .58$.

Figure 5

Recollection component during the item recognition phase



Note. Stimulus-locked ERPs during the item recognition phase. A. Color-coded ERP grand average recorded at parietooccipital electrodes with highlighted time window in gray. B. Topographical map plot of remembered violation minus forgotten violation difference in the recollection component time window.

Familiarity Component Amplitude During Retrieval

First, we conducted linear mixed effects models to investigate the effects of violation and item accuracy on the familiarity mean amplitudes obtained at frontocentral electrodes within 300 ms and 500 ms. Starting from the full model to the reduced model, there was no significant decrease in the model fit, $\Delta\chi^2(18) = 8.20$, $p = .98$. The main effects of violation, $\chi^2(1) = .66$, $p = .42$, and item accuracy, $\chi^2(1) = 1.00$, $p = .32$, and the interaction effect, $\chi^2(1) = 1.78$, $p = .18$, were non-significant. CBPT analysis comparing the remembered and forgotten non-violation trials did not find a cluster.

Discussion

The aim of this study was to investigate the electrophysiological correlates of encoding and retrieval of events eliciting PE. To achieve this, we employed a statistical learning task, whereby participants learned pairs of objects. Subsequently, their memory was tested for predictions that were violated. Our behavioral results revealed successful learning of the object pairs. However, contrary to our pre-registered hypothesis and prior findings (Bein et al., 2021), we did not observe a memory advantage for items giving rise to PE. Based on our ERP results, during retrieval, we found a significant association between the recollection component and item recognition memory for previously violated items. Specifically, there was a significant interaction, with higher amplitudes of the recollection component for remembered violation trials compared to forgotten violation trials, but no difference between remembered and forgotten non-violation trials. The results did not yield supporting evidence for the frontal negative familiarity component. Furthermore, our data also did not show a link between P3 mean amplitude during encoding, PE, and subsequent memory. Overall, these findings suggest that recollection influences the interplay between PE and episodic memory. Lastly, our exploratory analysis showed that our pre-registered time windows for ERP components aligned with the cluster-permutation results, indicating the validity of our approach in selecting relevant time-windows of interest[9].

In line with our pre-registered hypothesis, we found higher amplitude values from 400 ms to 800 ms at parietooccipital electrodes for remembered violation trials compared to forgotten violation trials, indicating a recollection effect during retrieval of items that previously elicited PEs. This recollection component suggests that retrieval of PE might involve the assessment of specific details of an episode. Notably, we observed a significant interaction effect, revealing a substantial difference in mean amplitudes of recollection component, specifically between remembered and forgotten violation items, but not within the non-violation items. This finding suggests that the violation of expectations can enhance recollection, aligning with previous behavioral research demonstrating the retrieval-enhancing effects of PE (Kafkas & Montaldi, 2018). The lack of a significant difference in the non-violation condition implies that the mere presentation of baseline items may not be sufficient to enhance recollection. This could be because novel items, in the absence of a strong violation, fail to engage deeper levels of processing, such as retrieving episodic details of an event (Cowell et al., 2019).

Our results regarding the recollection component contributes to the growing body of evidence supporting the notion that memory-guided predictions can enhance memory performance (Fenerci & Sheldon, 2022; Henson & Gagnepain, 2010; Theobald et al., 2022; Van Kesteren et al., 2012). Memory-guided predictions refer to the process by which retrieved memories of past events influence and shape predictions during the comprehension of unfolding events. For instance, Wahlheim et al. (2022) conducted a study investigating the effects of predictive-looking errors on remembering event changes. Predictive-looking errors

[9] The CBPT not only allowed us to identify significant effects but also served as a confirmatory tool, validating our choice of time windows for investigating the ERP components (Frömer et al., 2018).

occur when viewers direct their gaze to incorrect locations based on their memory of past experiences, but the actual event deviates from their predictions. In their study, participants watched movies of everyday activities, including actions that were repeated either identically or with changed features. Their findings demonstrated that memory guidance led to predictive-looking errors, which were associated with better recollection memory for changed event features. This suggests that retrieving recent event features can guide predictions during unfolding events, and PE can contribute to enhanced recollection when it is driven by expectations. In line with these findings, we observed a recollection effect only for violation items, which were presented instead of the second object of the pairs that the participants had predicted to see. Taken together, our findings show that deviations from what was expected generate a stronger recollection signal that may facilitate better subsequent memory.

In contrast to previous studies that have demonstrated better memory for events eliciting PE (Antony et al., 2021; Bein et al., 2021; Brod et al., 2018; Greve et al., 2017; Quent et al., 2022), our study, despite utilizing a similar setup (Bein et al., 2021), revealed a more nuanced pattern. We did not observe an overall memory advantage for PE, but only differences in the neural correlates of retrieval of events that elicited PE. The behavioral observation is also consistent with recent studies that did not show memory-enhancing effect of PE (Nolden et al., n.d., Ortiz-Tudela et al., 2023; Turan et al., 2023). Thus, it is reasonable to consider that there may be additional factors moderating the relationship between PE and subsequent memory benefit. Factors such as the strength and the precision of the prior (Greve et al., 2018; Ortiz-Tudela et al., 2023), the appraisal (Gruber & Ranganath, 2019) and the novelty (Schomaker & Meeter, 2018) of the violation could potentially influence the effect of PE on memory. In the following, we will discuss these factors and provide potential explanations for their presence in our results.

Our study protocol was similar to a previous study that demonstrated the beneficial effect of PE on memory (Bein et al., 2021). However, there was a main difference between our study and the study by Bein et al.'s (2021) which was the increased number of object pairs and blocks. To ensure an adequate signal-to-noise ratio for the EEG signal, we increased the number of trials from 36 to 50 for each condition, necessitating additional blocks and sessions to achieve an effective learning threshold. Consequently, our extended learning phase likely resulted in stronger predictions compared to the previous study (Bein et al., 2021), where the reported accuracy rate was .60, whereas in our study, it was .78. As a result, our participants may have had stronger predictions, leading to higher item surprise for violation trials (Greve et al., 2017; Quent et al., 2021). It is reasonable to assume that stronger predictions are associated with higher PE and that might have resulted in improved subsequent memory. However, according to a recent framework (PACE: Gruber & Ranganath, 2019), the memory enhancement for PEs is not solely determined by prediction strength but also by appraisal. This framework proposes that PE triggers an appraisal process that influences one's actions and subjective experience in resolving the uncertainty elicited by PE. This process can either trigger curiosity and subsequent memory enhancement or elicit behavioral inhibition due to negative uncertainty assessment. In our study, participants may have exhibited a tendency to disregard the new objects altogether, violation and non-violation objects presented during the violation phase, instead relied more heavily on the previously learned objects, possibly indicating a negative assessment of uncertainty resolution. Congruently, a similar finding was reported in one of our recent studies (Ortiz-Tudela et al., 2023), which demonstrated a decreased memory performance for violations of strong predictions derived from low-uncertainty priors. Furthermore, the role of context surprise (Quent et al., 2021) should be taken into account when interpreting our findings. Our task involved extensive exposure to the paired structure of object associations, which could have created context surprise when participants encountered a non-violation item that violated the expected task structure. Specifically, violation items violated the expected object at the item level, whereas non-violation items violated the expected task structure by presenting an object that had not been previously seen in that specific position (i.e., after the second object of a pair), thereby creating a context surprise and leading to novelty. This distinction may have elicited different cognitive and neural responses compared to the violation items that violated the expected object at the item level. Therefore, the absence of a memory benefit for PE and its relationship to the P3 component in our study could potentially be attributed to both experimental conditions engendering expectations and subsequent violations of those expectations (Schomaker & Meeter, 2018).

In conclusion, our results highlight the importance of recollection in the mechanisms underlying the association between PE and episodic memory processes. It is important to note that solely relying on behavioral data from our study may not provide a complete understanding of the effect of recollection. Further investigation into the recollection effect could provide a more comprehensive understanding of how PE influences memory. Moreover, future research could consider additional factors that moderate the relationship between PE and memory benefit, such as the strength and the precision of priors, appraisal, and novelty of the violation (Greve et al., 2018; Gruber & Ranganath, 2019; Ortiz-Tudela et al., 2023; Schomaker & Meeter, 2018). Overall, our study contributes to the growing body of knowledge on the complex and nuanced nature of the relationship between PE and episodic memory processes, shedding light on the underlying neural mechanisms involved.

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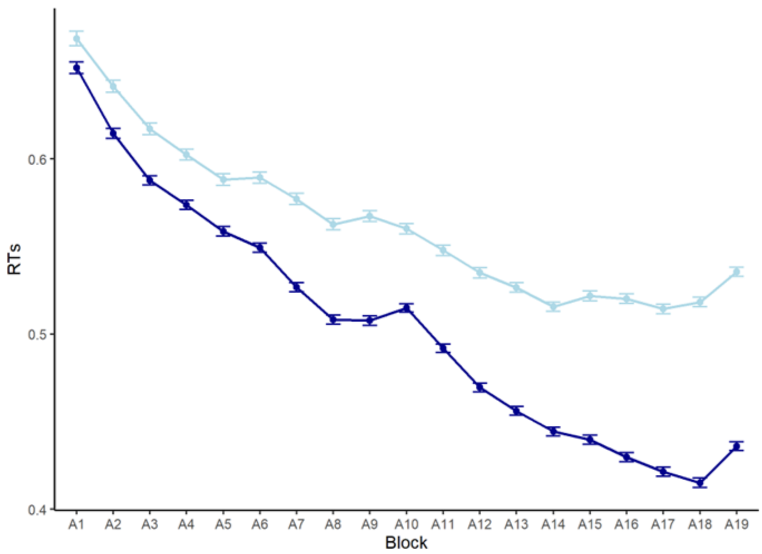
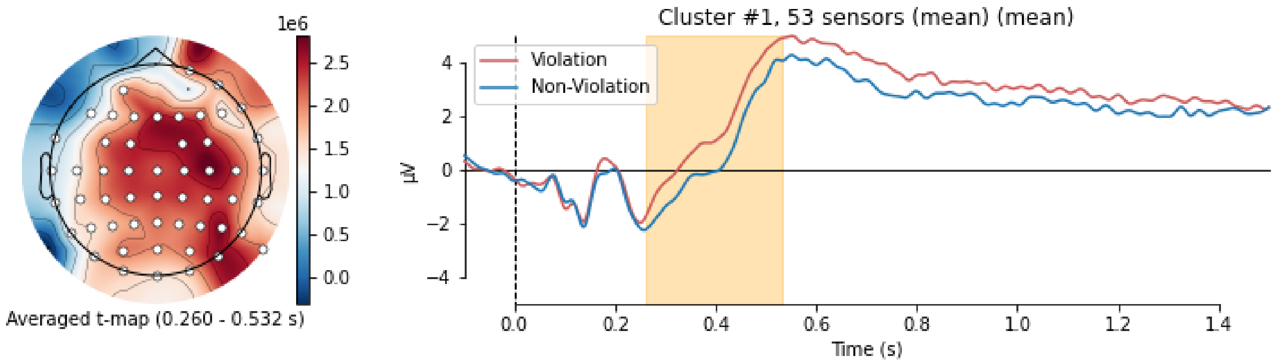
Appendices

A. RT differences between the first and second item of the pairs during the prediction learning and reminder phases.
B. CBPT results for the P3 mean amplitude for the comparison violation and non-violation trials.
C. CBPT results for the recollection component for the comparison remembered violation and forgotten violation trials.
D. CBPT results for the recollection component for the comparison remembered non-violation and forgotten non-violation trials.

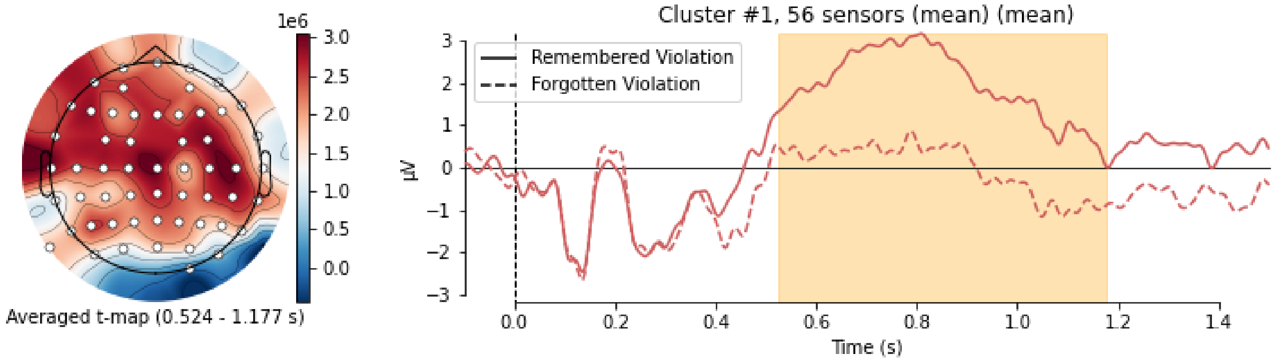
A.



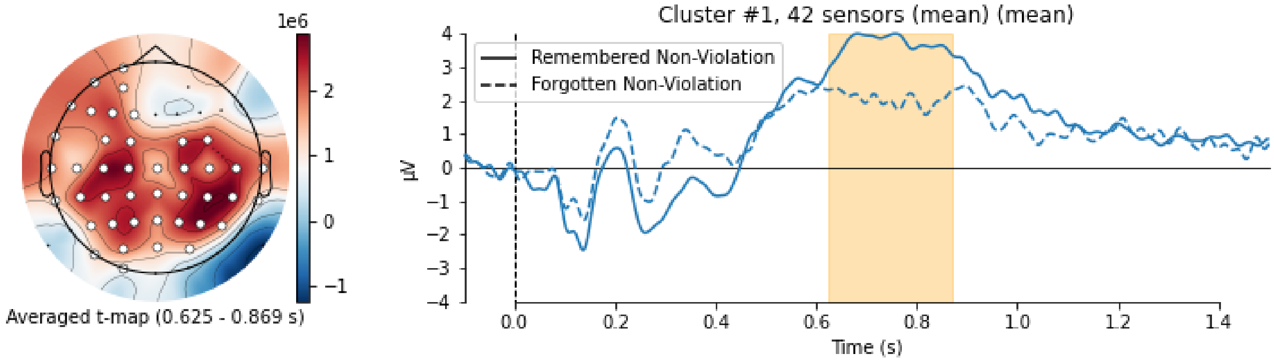
B.



C.


1e6
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Averaged t-map (0.524 - 1.177 s)
Cluster #1, 56 sensors (mean) (mean)
Remembered Violation
Forgotten Violation
µV
Time (s)

D.


1e6
2
1
0
−1
Averaged t-map (0.625 - 0.869 s)
Cluster #1, 42 sensors (mean) (mean)
Remembered Non-Violation
Forgotten Non-Violation
µV
Time (s)

Author contributions: Author contributions are codded according to the CRediT taxonomy (Allen et al., 2014).

Gözem Turan: Conception, Methodology, Computation, Formal Analysis, Investigation – performed the experiments, Investigation – data collection, Data curation, Writing – writing the initial draft, Writing – review & editing, Writing – visualization, Project Administration

Veronika Spiertz: Investigation – data collection, Data curation, Writing – review & editing

Oded Bein: Conception, Methodology, Resources, Writing – review & editing

Yee Lee Shing: Conception, Methodology, Writing – review & editing, Supervision, Project Administration, Funding Acquisition

Sophie Nolden: Conception, Methodology, Writing – review & editing, Supervision, Project Administration, Funding Acquisition

Acknowledgments: The study was funded by a Starting Grant from the European Research Council for YLS (ERC-2018-StG-PIVOTAL-758898). The work of YLS was also supported by the German Research Foundation (Project-ID 327654276, SFB 1315, "Mechanisms and Disturbances in Memory Consolidation: From Synapses to Systems"), and the Hessisches Ministerium für Wissenschaft und Kunst (HMWK; project "The Adaptive Mind"). The work of SN was also supported by a Research grant Focus A/B, Goethe-University Frankfurt am Main, ("Dynamics of auditory and visual memory representations in the aging brain"). We would like to thank our student assistants Daniel Urban, Johanna Diehl, Margo Schleuter, Melek Yalcin, Noah Mba, and Pauline Drexel for their help with data collection and all study participants for their time and effort. We also thank all members of the LISCO Lab (PI: YLS) for helpful feedback and discussion on the study. The authors are grateful to Dr. Sebastian Korinth for his generous support on technical issues during the recordings.

Data Availability: Data, scripts, and additional online materials are openly available at the project's Open Science Framework page (https://osf.io/sbc7d/).

Conflict of Interest: We have no conflicts of interest to disclose.

Original Manuscripts – Study 3

The impact of mnemonic prediction errors on episodic memory: A lifespan study

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Abstract

Memory-derived predictions help us to anticipate incoming sensory evidence. A mismatch between prediction and evidence leads to a prediction error (PE). Previous research suggested that PEs enhance memory of the surprising events. Here, we systematically investigated the effect of PE on episodic memory in children (10-12 years old), younger adults (18-30 years old), and older adults (66-70 years old). Participants learned visual object pairs over two days. On Day 3, new objects were shown among the pairs, either after the first item of a pair (violation items), i.e., instead of the second item, or between pairs (non-violation items), i.e., when no specific predictions were possible. Our results did not reveal a significant boosting effect of PE on memory in any of the age groups. In contrast, in children, violations resulted in lower memory specificity compared to non-violations. Older adults showed lower memory specificity than the other age groups across violations and non-violations. We conclude that the beneficial effect of PE on episodic memory may be less consistent than theoretically postulated and may not always be observed in experimental settings involving statistical learning and item-specific violations, and that children's memory specificity may indeed suffer from PE.

Keywords: Prediction error; episodic memory; memory specificity; associative learning; lifespan; development

The impact of mnemonic prediction errors on episodic memory: A lifespan study

Throughout the lifespan, humans are constantly confronted with changing environments. What was once stable might change, which requires adaptation to new situations. This process may entail dynamic mental representations that comprise sequential information. Imagine a person who wants to get to a store that she typically reaches by first taking the bus to the city center, and then taking the tram. After making the same route several times, she has integrated the bus and the tram parts of her trip into memory. Upon arriving to the city center, she could already predict the tram and maybe some of its details. However, sometimes predictions are not met, and one may experience prediction errors (PEs). For example, if there is construction work, she might need to substitute the tram part with a rental bike. Learning from PEs are particularly important for adaptive behavior in our changing environments. Thus, it is important to remember the events that generated them and integrate these events into our preexisting knowledge, or modify the knowledge (Frank and Kafkas, 2021; Henson & Gagnepain, 2010; Quent et al., 2021).

There is some evidence that PE may lead to distinct memory traces (Frank et al., 2020; Gershman et al., 2014; Love et al., 2004). In addition, it has been shown that events that give rise to PEs are remembered better than events that do not (Antony et al. 2021; Brod et al. 2018; Greve et al. 2017; Kafkas & Montaldi, 2018; Kalbe & Schwalbe, 2021). In a recent study with young adults (Bein et al., 2021), participants incidentally learned associations between sequentially presented pairs of objects. Pairs were shown repeatedly, with the assumption that participants would eventually predict the second item of a pair when seeing the first item of a pair (Kim et al., 2014, 2017). In the encoding phase that followed, these predictions were violated in some cases by showing a different item at the second position. A later memory test revealed that these violation items were remembered better than comparable items that did not violate predictions (Bein et al., 2021, but see also Ortiz-Tudela et al., 2023; Turan et al., 2023).

Situations in which memory-derived predictions are violated, and thus knowledge update is required, can occur at any point in life. However, studies examining the effect of PE on memory in different age-groups are lacking. It is important to shed light on such fundamental learning and memory processes over the lifespan to better understand how a dynamic environments shape the memories of children, younger adults, and older adults, and to infer how age-adequate learning environments could be constructed. In the current study, we aimed to fill this gap by having children, younger adults, and older adults perform a statistical learning task combined with events that give rise to PEs, very similar to the paradigm by Bein et al. (2021). Participants learned associations between objects that had no semantic relation, such that age-related differences in knowledge were controlled for. These associations were then used as the basis for mnemonic predictions that were sometimes violated. The goal of the current study was to isolate age-specific memory effects of remembering items related to PEs.

According to the two memory components framework (Shing et al. 2008, 2010; Shing & Lindenberger, 2011), mechanisms underlying episodic memory differ across the lifespan. The two interacting components refer to (i) an associative component, which is responsible for binding and is related to hippocampal development; (ii) a strategic component, which mediates mnemonic control processes and is related to prefrontal cortex development (e.g., Ofen et al., 2007, Nolden et al., 2021). The developmental trajectories of these two components differ across the lifespan, such that the associative component develops relatively faster than the strategic component in childhood, whereas both components decline in a similar way in older age. In other words, the two-component framework suggests that children rely relatively more on the associative component of episodic memory, creating bound representations which may eventually be used to generate predictions. Due to this bias towards the associative component, events eliciting PEs may be especially salient for children, leading to more pronounced PEs, and presumably also relatively better memory for these events, than in adults.

Evidence supporting the idea that PEs might especially benefit memory at a younger age comes from a recent study showing that 9-11year-old children remembered facts better when they made an (often incorrect) prediction compared to providing an example. This difference was less pronounced in younger adults (Breitwieser & Brod, 2021). In their study, the authors used a numerical-facts learning task to compare the effectiveness of two learning strategies, that is (i) making a prediction and (ii) example generation. For the prediction condition, the participants were asked to provide answers for questions, for example, how many animals out of ten are insects. On the other hand, for the example condition, the participants had to think about an example of an insect. The results showed that generating predictions led to better memory performance in children than generating examples, while both strategies were similarly effective in adults. Hence, based on current theory and empirical data, the effects of PE on memory may be magnified in children.

On the other end of the lifespan, older adults may be less sensitive than younger age groups to the effects of PE on memory. Given that the associative component declines in old age, and related to this, predictions based on remembered associations presumably decline as well, the effect of PE on memory may be reduced. In addition, fluid abilities have been shown to decline over the lifespan and crystallized knowledge becomes more important (Baltes et al., 1999; Cattell, 1971, Li et al., 2004). This could suggest a less malleable knowledge structure, such that the effects of PE on episodic memory may be less pronounced in older adults, compared to younger adults and children.

When investigating the effect of PE on memory, it is particularly important to examine whether PE affects the details remembered (e.g., Frank et al., 2020 for a study with younger adults). When testing memory with a mnemonic similarity task, one can draw conclusions on how detailed or gist-like memories are. In this memory test, participants are required to indicate whether an item is identical to that they have seen during encoding, or whether it is similar, but not identical, or new. When memory is gist-like, identical old and similar items might be confused. However, if one has detailed memory of the item they saw during encoding, old versus similar items can be accurately classified. Pattern separation, a process by which distinct representations are allocated to similar information and that is thought to mediate high-fidelity detailed memories, was shown to decline in older adults (e.g., Doxey & Kirwan, 2015; Holden et al., 2013; Stark et al., 2013). Consistent with that, sensory memories evoke less specific brain activity in older adults compared to younger adults (neural dedifferentiation, e.g., Koen et al., 2020, Koen & Rugg, 2019; Park et al., 2004; Voss et al., 2008). A critical question is thus whether PE, which might boost memory specificity (at least in younger adults; Bein et al., 2021), could attenuate reduced memory specificity in aging.

In the current study, we aimed to systematically compare the effects of PE on memory across different age groups. One challenge is the difference in the amount of knowledge between age groups. Children have the least knowledge of the world and constantly need to acquire and update their knowledge structures. On the other hand, younger and older adults may be similar in the amount of knowledge, but older adults seem to rely more heavily on this knowledge than younger adults (Horn & Cattel, 1967; Horn & Hofer, 1992). Thus, one of the key components of the current study is that we taught participants sequential associations during the experiment through intensive training. After training, novel items were introduced in positions where they either violated predictions or not. Memory for these novel items was tested in a recognition test comparing memory of identical old items, similar lures, and new items. We expected better memory for items that violated predictions compared to items that did not violate predictions (Bein et al., 2021). Regarding the age effects, we expected the greatest difference in the effect of PE on memory in children, followed by younger adults, and the smallest effect in older adults.

Methods

This study had been preregistered prior to data collection. (The link to the preregistration will be made available at publication in order to enable an anonymous review process.)

Participants.

Seventy-five children (10-12 years old), 48 younger adults (18-30 years old), and 50 older adults (66-70 years old) took part in this online study. Participants were recruited through our participant data bank, advertising sheets and posters, the institute's digital recruitment platform, and personal contact.

The data of 21 children was excluded because of incomplete data (6 participants decided to not continue, 8 participants experienced problems when executing the software, and in 7 cases the data was not completely saved due to technical errors). The data of 7 further children was excluded due to errors during task execution made by experimenter or participants. The data of 4 younger adults was excluded because of incomplete data (1 participant experienced problems when executing the software, and in 3 cases the data was not completely saved due to technical errors). One additional younger adult was excluded due to misunderstanding of the task. The data of 3 older adults were excluded because of incomplete data (1 participant decided to not continue, 1 participant experienced problems when executing the software, and in 1 case the data was not completely saved due to technical errors). The data of 6 further older adults was excluded due to errors during task execution, driven by experimenter or participants. In the final sample, there were 47 children (mean age = 11.06 years, range: 10-12 years; 23 girls, 24 boys), 43 younger adults (mean age = 22.56 years, range: 18-30 years; 32 women, 11 men), and 41 older adults (mean age = 67.63 years, range: 66-70 years; 20 women, 21 men).

All participants spoke German or English as their native language or at level close to native language. The instructions were given in German or English, depending on the participants' preference. All participants received 8 € per hour or course credit for their participation and gave informed consent. The study was approved by the ethics committee of University where the research was conducted.

Power analysis. Prior to data collection, a power analysis was conducted with g*power (Faul et al., 2007). The effect size for the interaction (violation/non-violation, age group) was estimated to be 0.25 at the standard .05 alpha error probability in order to obtain .80 power, based on conservative consideration of the effect sizes reported in Bein et al. (2021). Additionally, a power analysis was conducted using an R package titled WebPower (https://webpower.psychstat.org) to confirm the sample size estimation. Based on these analyses, we targeted to collect usable data from 120 participants, 40 for each age group.

Stimuli.

Our stimulus set included pictures of everyday nameable objects, and was nearly identical to the stimulus set of Bein et al., (2021, based on DuBrow & Davachi 2013; Kuhl et al. 2011; Polyn et al. 2005; Tompary & Davachi 2017). In very few cases, we replaced pictures of objects that may be uncommon in Germany (compared to the USA; e.g., air conditioner) with other pictures. Objects were presented in a 350 x 350 pixels white square on gray background and were sized to maximize the size of the objects without distorting proportions. The items were shown as predictive pairs that were intended to build up predictions, violation and non-violation items that were introduced during the violation phase, and new items that were used in the recognition test. A set of 180 pictures was used, from which 144 stimuli were randomly selected to be used as predictive pairs, and 36 stimuli to be used as new items during the recognition test. Half of them were big items and the other half were small items, defined as being bigger or smaller than a shoe box. Each predictive pair consisted of a big and a small item, and in half of the pairs, the big item of a pair was presented before the small item, vice versa in the other half of the pairs. The violation and non-violation items (32 each) as well as their similar lures were randomly chosen from another set of 72 objects, that each existed twice such that there were two similar but distinguishable pictures of the same object (144 items in total in this picture set). In the violation phase, both violation and non-violation items were always of different size category than the previously presented item (big or small). This is so that, in case of violation items, only the item itself violated the expectation while the size category and the correct responses remained the same. Half of the violation and non-violation items were shown both in the violation phase as well as during the recognition test as targets, whereas the other half of the violation and non-violation items were only shown during the violation phase and the respective similar lure (same object but different exemplar) was shown in the recognition test as similar lures.

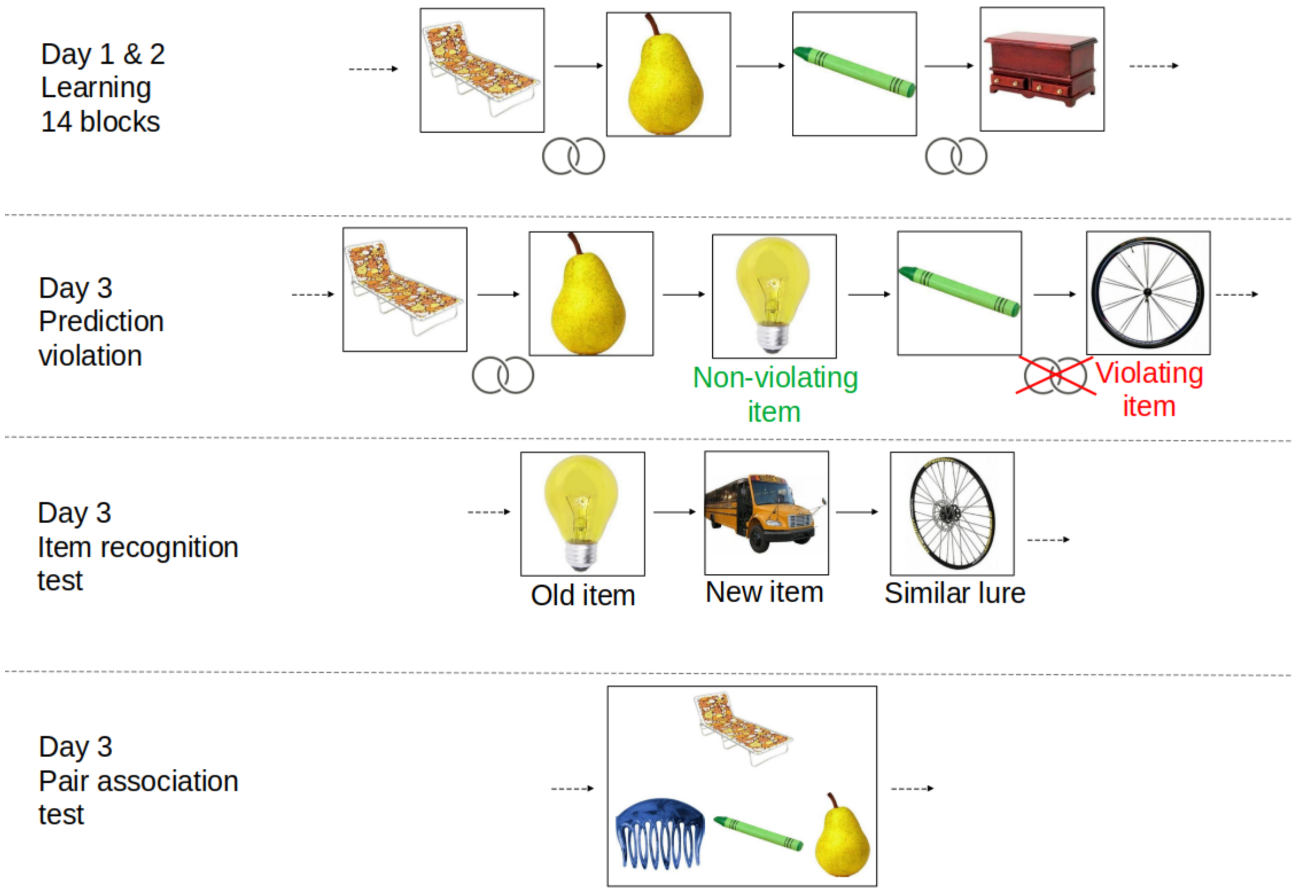
Procedure.

The study was done completely online due to the COVID-19 pandemic when onsite testing was not possible. Trial lists containing information on the stimuli and stimulus categories to be shown were created with custom Matlab scripts (R2021b). The tasks themselves were programmed in PsychoPy (Peirce et al., 2019) and uploaded to Pavlovia (pavlovia.org). Participants downloaded the tasks via links that they received from us. As the study was conducted online due to the pandemic, additional procedures were taken to ensure data quality (Newman et al., 2021). At the beginning of session on each day, the experimenter video called the participants to check their well-being and physical environment. All participants were instructed to be in a quiet room, sit in a comfortable chair, use a computer with a stable internet connection, and minimize distractions. Participants performed the study on their personal computers or laptops on a keyboard, not on cell phones or tablets. Also, before the study, our participants were familiarized with the online procedure through instructional videos that can be found in our lab's webpage (www.psychologie.uni-frankfurt.de/102061001/Instructions_for_Online_Testing___English_Version). During the video call, the experimenter explained the task. To make the task more interesting for kids, there was a cover story in which an architect and an engineer guided the participants through the blocks and introduced the individual tasks. The practice trials were presented using a slide show that the experiment shared on the screen with the participants.

The study took place on three consecutive days, with the sessions taking place roughly at the same time of the day. On Day 1 and Day 2, participants learned the predictive pairs in the bigger-or-smaller task (learning phase). On Day 3, participants started again with the bigger-or-smaller task, that comprised a reminder phase and the violation phase. Afterwards, participants did an item recognition test, a math distractor task, and an associative memory test (see Fig. 1).

Figure 1

Tasks and procedure.



Note. **(First row).** During learning on Day 1 and Day 2, participants indicated, for each trial, if the current picture was bigger or smaller than the previous one in real life. There was a hidden sequential structure, such that two items made a pair with invariant order, while the order of pairs was randomized in each block. We expected participants to eventually predict the 2nd item of a pair at the occurrence of the 1st item of a pair. **(Second row).** During the violation phase on Day 3, participants performed the bigger-or-smaller task as in the learning phase. New objects were presented in between pairs (non-violation items) or they replaced the 2nd item of a pair (violation items). **(Third row).** During the item recognition test, participants classified items as old, similar, or new. Apart from new items, non-violation and violation items or their respective similar lures were presented. **(Fourth row).** During the pair association test, participants indicated which items had usually been shown in succession. The 1st item of a pair was presented as cue; there were three alternative choices for the 2nd item, with one of them being the correct one.

Learning phase. Participants completed 14 blocks of the bigger-or-smaller task, seven blocks on Day 1 and seven on Day 2 (see Fig. 1). In each block, the 144 items were presented consecutively and participants had to indicate if the present object was bigger or smaller than the previous one, by pressing the right or left arrow key, respectively. Participants were informed that during the experiment all objects have relatively the same size on the screen, but that they should make their judgments based on the real-life sizes of the objects. They were additionally asked to respond as quickly as possible, while still being accurate. No response was expected for the first item of a block. Unbeknownst to the participants, items were organized in pairs, such that the items of each pair were always presented consecutively and in the same order in all the blocks. Thus, participants could implicitly learn to predict the second item of a pair after the first item (see also Kim et al. 2014, 2017; Schapiro et al. 2012; Turk-Browne et al. 2012). The order of the pairs was randomized across blocks. Each item was presented for 1.5 s and was followed by a fixation cross located at the center of the screen for an interstimulus interval (ISI) of 2.5 s. Below the picture, we presented a left-pointing arrow and small circle (on the left side), and a right-pointing arrow and big circle (on the right side), to remind participants of the possible responses. These disappeared as soon as a response was made. Responses could be made from the stimulus onset until the next trial. Between blocks, participants could take self-paced breaks of 15 s to 3 minutes in duration. Before participants started the main learning task on both Day 1 and Day 2, they did 10 practice trials with the help of the slide show shared by the experimenter. Responses during practice were given verbally and practice was repeated if participants gave less than 6 correct answers on the bigger-or-smaller task. All participants completed the practice trials successfully with very few cases of repeated practice needed.

Reminder and violation phases. Day 3 started with the reminder and the violation phases (see Fig. 1). From the perspective of the participants, the task did not change. They were again asked to complete the bigger-or-smaller task during both phases, with the same timing and response options as during learning. Again, this task was preceded by 10 practice trials. The first block was a reminder block, in which the 72 pairs were shown again to refresh the memory of the learned pairs. After the reminder block, four violation blocks followed. Each of these blocks contained 18 of the originally learned pairs. Each pair was first presented intact, and then a second time either with a violation item that replaced the second item of the original predictive pair (for half of the pairs), or with a non-violation item that simply followed the second item of a pair (for the other half of the pairs). In the violation condition, we assumed that participants predicted to see the second item of the pair after seeing the first item, and that this prediction was violated when the violation item showed up instead. In the non-violation condition, we assumed that participants would not predict to see a specific item after the second item of a pair, thus the non-violation item did not violate a prediction. The presentation of the intact pairs, the violated, and the non-violated pairs was randomized, with the constraint that there were at least six intervening pairs between an intact pair and its second occurrence as a violated or non-violated pair.

Item recognition test. The item recognition test followed the violation phase (see Fig. 1). Participants were asked to classify items as old, new, or similar. They saw 18 violation trials exactly as they were presented during the violation trials (old violation items), and 18 violation trials as similar lures, that is the same object as originally presented, but a different exemplar. Similarly, 18 old non-violation items and 18 similar non-violation trials were presented, alongside 36 new items. The items were distributed across two blocks with identical proportions. The order of the items within each block was randomized. The items were presented on the center of the screen for 3 s, followed by a fixation cross of 3 s.

Participants responded with the left arrow key, the down arrow key, and the right arrow key, using the ring, middle, and index finger of the right hand. “Similar” responses were always given with the down arrow key. The mapping of the left or right arrow key to “old” or “new” responses was counterbalanced across participants. The participants could respond as soon as the item was shown and until the beginning of the next trial. Below the image, arrow symbols with the respective response words appeared to remind participants of the possible responses and their mapping to the arrow keys. They disappeared as soon as a response was made. Before the recognition test, participants completed 12 practice trials.

Math distractor task. Participants were asked to complete simple mathematical tasks for three minutes. An equation was shown in the center of the screen, alongside three possible response options depicted below. Participants were asked to select the correct response via the “A”, “S”, or “D” keys on their keyboards. They were asked to respond with the ring, middle, or index finger of their left hand. The letters “A”, “S”, and “D” were depicted under the three response options in order to point to the respective response keys. The equation stayed on the screen until the participants responded. After 500 ms, the next equation was shown. The task stopped automatically after 3 minutes. A different set of equations was used for children than for younger and older adults.

Associative memory test. This task targeted explicit memory of the originally learned predictive pairs of Day 1 and Day 2 (see Fig. 1). The first item of each pair was presented centrally in the upper part of the screen, and three different items were presented next to each other in the lower part of the screen, one of them being the second item that belonged to the same pair as the item in the upper part of the screen. The other two items were also taken from the set of originally learned pairs. Participants were asked to select the correct second item by pressing “A”, “S”, or “D” with the ring, middle, or index finger of their left hand. As in the math distractor task, the letters “A”, “S”, and “D” were depicted under the three response options, alongside a short description of the task. The letters and the description disappeared as soon as a response was made. The items were shown for 5 s, followed by a fixation cross for 1 s. Participants could respond as soon as the items were shown, and until the next trial started. Before the associative memory test, participants completed 8 practice trials.

Design and analyses.

Exclusion criteria. Participants' data were excluded if they showed very poor performance in the recognition test, defined as recognition memory performance (hit rates for old items minus false alarm rates for new items < .05). Hits were defined as old or similar responses to old items. This exclusion criterion was preregistered. In addition, we realized during data collection that not all participants, especially among the children, were able to remain focused throughout the bigger-or-smaller task. Thus, we excluded data if performance was less than 85 % correct during learning or during the reminder and violation phase. We only looked at accuracy for the second item of a pair because the first and second items of a pair were always from different size categories (big, small), and thus, the decision should be easy to make. Based on the criteria, we excluded the data of 11 children (mean age of the remaining children = 11.11 years; 20 female and 16 male children remaining), four younger adults (mean age of the remaining younger adults = 22.54 years; 28 female and 11 male younger adults remaining), and one older adult (mean age of the remaining older adults = 67.62 years; 20 female and 20 male older adults remaining).

Analyses of response rates. Three preregistered analyses on the rates of "old" responses in the recognition test, to compare the current study to the results of Bein et al. (2021). First, in an analysis without any filters, the effects of three independent variables were examined with a mixed ANOVA. The between-subjects variable was age group (children, younger adults, older adults), and the two within-subjects variables were violation (non-violation items, violation items) and test item (old, similar).

Second, the analysis just described was repeated, but including only violation items for which the participants explicitly remembered the corresponding pair in the associative memory test. The rationale was to only include trials in which participants encoded the predictive pairs, and thus presumably had strong predictions and strong PEs when the violation occurred. A similar approach was taken by Bein et al. (2021). To ensure there were enough trials per condition, only the data of participants with an average associative memory performance > .38 % was included. This criterion led to the additional exclusion (only for this particular analysis step) of eight children (mean age of the remaining children = 11.18 years; 16 female and 12 male children remaining), seven younger adults (mean age of the remaining younger adults = 22.75 years; 23 female and 9 male younger adults remaining), and fourteen older adults (mean age of the remaining older adults = 67.69 years; 11 female and 15 male older adults remaining).

Third, the same analysis was modified such that items were differentiated based on the decrease in response times (RTs) for the corresponding predictive pair during learning. We relied on the notion that decrease in RT reflects learning. Thus, we reasoned that pairs that show a larger RT decrease might reflect better learning, and potentially strong predictions and strong PEs in face of a violation. Given that the explicit memory test is done after learning, we thought that response times *during learning* might be more effective in revealing differences between strong and weak predictions. For the second item in each pair, we calculated the difference in RT between the first learning block and the last learning block. This difference controls for RT that is just due to responding to this item and allows us to look specifically at the change due to learning. We then created two bins of items based on a median-split: items with larger RT decrease were considered as stronger predictions, whereas items with smaller RT decrease were considered as weak predictions. The same analysis as above was repeated, but including this prediction strength variable. This resulted in the between-subjects variable age group (children, younger adults, older adults), and the three within-subjects variables RT savings (strong, weak), violation (non-violation items, violation items) and test item (old, similar). Trials with missing responses or RT outliers (responses faster than 50 ms, responses +/- 3 SD from participants' average RTs) were not analyzed. The data of one additional child was excluded from this analysis due to too few trials to meaningfully calculate learning RT decrease for all other conditions (mean age of the remaining children = 11.11 years; 19 female and 16 male children remaining).

Confusion matrix analysis. In addition to the analyses of the response rate, the data was analyzed using confusion matrices (Ngo et al., 2021) to account for possible age-specific response biases and to better delineate the effects of pattern separation between the age-groups. This analysis was not preregistered. For violation and non-violation items separately, precision was calculated (e.g., for old items: rate of correct old responses divided by all old responses, see Fig. 2) and sensitivity (e.g., for old items: rate of correct old, responses divided by all old items) for old classifications. Naturally, new items could not be divided into the violation vs. non-violation items. Precision and Sensitivity were used to calculate F1 scores which were the basis for indices for old and similar classifications (see Fig. 2). These indices were submitted to linear mixed effect models (modeled in lmer for R) with violation and age group as fixed effects and participant as random effect.

Figure 2

Confusion matrices and calculation of classification indices.

		Response		
		Old	Similar	New
Item type	Old			
	Similar			
	New			

		Response		
		Old	Similar	New
Item type	Old			
	Similar			
	New			

Note. For both old and similar items (left and right panels, respectively), an F1 score based on precision and similarity was calculated. The relevant rows and columns of the matrices are highlighted in red and blue.

Precision = correctly identified items (black cell) / all responses of this type (black and blue cells)

Sensitivity = correctly identified items (black cell) / all items of this type (black and red cells)

F1 score = 2*Precision*Sensitivity/(Precision+Sensitivity)

Index for old classifications: F1 score minus rate of new responses to old items

Index for similar classifications: F1 score minus rate of old responses to similar items

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Deviations from the preregistered protocol.

There were deviations from the original plan (e.g., Claesen et al., 2021; Nosek et a., 2019). First, due to aforementioned problems related to exclusion criteria, online testing, and data transmission, additional participants had to be recruited. Secondly, an additional exclusion criterion was introduced due to poor performance during the bigger-or-smaller task, which was found to be challenging for some participants, mostly for the children. This criterion was added to the preregistered exclusion criteria. Lastly, we further analyzed the confusion matrices (Ngo et al., 2021), since it has been considered as more sensitive than the response rate analyses in accounting for age-specific response biases and the effects of pattern separation and completion between different age groups.

Results

Analyses of response rate in recognition test.

A mixed ANOVA for 'old' responses, with the between-subjects variable age group (children, younger adults, older adults), and the within-subjects variables violation (non-violation, violation) and test item (old, similar) on old response rate (see Fig. 3) revealed a significant main effect of age group, $F(2, 112) = 15.71$, $p < .001$, $\eta_g^2 = .14$, a significant main effect of test item, $F(1, 112) = 582.78$, $p < .001$, $\eta_g^2 = .56$, and a significant interaction of age group and test item, $F(2, 112) = 3.21$, $p < .05$, $\eta_g^2 = .01$. To decompose the interaction, mixed ANOVAs were conducted with the within-subjects variables test item (old, similar) and age group, whereas each time two of the three age groups were contrasted to each other. A significant interaction of age group and test item was revealed when contrasting younger adults and older adults: $F(1, 77) = 7.43$, $p < .01$, $\eta_g^2 = .03$. This reflects a high proportion of old responses to similar items in older adults (children: $M = .20$; younger adults: $M = .19$; older adults: $M = .38$). All other effects of the main ANOVA were not significant (main effect of violation: $F < 1$[10], interaction of age group and violation, $F(2, 112) = 1.61$, $p > .20$, $\eta_g^2 = .00$, interaction of violation and test item, $F < 1$, three-way interaction, $F(2, 112) = 2.06$, $p > .13$, $\eta_g^2 = .00$).

Figure 3

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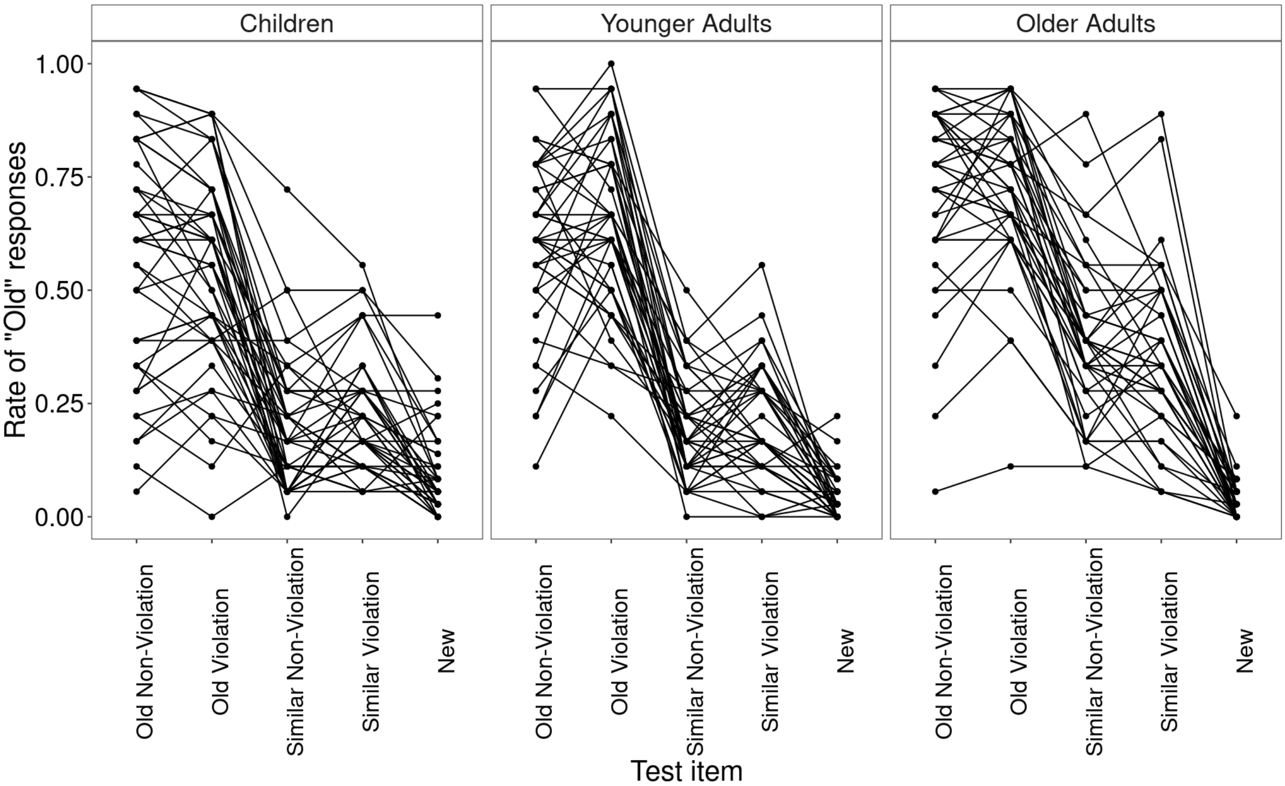
[10] Our analysis of response rate did not replicate the results by Bein et al. (2021). We thus also ran the exact analysis as reported in that paper. Participants with performance < .4 in the associative memory task were excluded from the analysis ($n = 8$), all trials with incorrect decisions in the associative memory task were removed from the analysis, and only younger adults' correct responses for old items were contrasted regarding violation. Performance was similar in non-violation (66%) and violation items (65%), and did not differ significantly, $t(34) = .12$, $p > .90$. We further calculated a Bayes factor with the "BayesFactor" package in R because the frequentist analysis pointed to a null effect. The Bayes factor was 0.18, thus, there was substantial evidence for the null hypothesis.

Response rates in the recognition test.



Note. Individual old responses across the different age groups.

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Next, the data was filtered to include only items for which the corresponding pair was remembered in the associative memory test. Overall, the pattern of results was similar to the first analysis. A mixed ANOVA with a between-subjects variable of age group (children, younger adults, older adults), and within-subjects variables of violation (non-violation, violation) and test item (old, similar) revealed a significant main effect of age group, $F(2, 83) = 7.90$, $p < .001$, $\eta_g^2 = .09$, a significant main effect of test item, $F(1, 83) = 542.61$, $p < .001$, $\eta_g^2 = .61$, and a significant interaction of age group and test item, $F(2, 83) = 4.11$, $p < .02$, $\eta_g^2 = .02$. To decompose the interaction, mixed ANOVAs were conducted with the within-subjects variables test item (old, similar) and age group, whereas each time two of the three age groups were contrasted to each other. A significant interaction of age group and test item was revealed when contrasting younger and older adults: $F(1, 56) = 8.78$, $p < .01$, $\eta_g^2 = .05$, due to a high proportion of old responses to similar lures, but not to old items, in older adults ('old' responses to similar lures: children: $M = .22$, younger adults: $M = .20$, older adults: $M = .38$. All other effects of the main ANOVA were not significant, main effect of violation: $F < 1$, interaction of age group and violation, $F(2, 83) = 2.43$, $p > .09$, $\eta_g^2 = .01$, interaction of violation and test item, $F < 1$, three-way interaction, $F < 1$.

In our third analysis, small and large RT savings were contrasted in a mixed ANOVA with the between-subjects variable age group (children, younger adults, older adults), and the within-subjects variables violation (non-violation, violation), test item (old, similar), and RT savings (small, large). To avoid redundancy, only effects concerning the variable RT savings will be reported. Neither the main effect nor any of the concerned interactions reached significance. The interaction of violation, test item, and RT savings showed a non-significant trend, $F(1, 111) = 3.47$, $p = .07$, $\eta_g^2 = .00$. To decompose the trend, mixed ANOVAs were conducted with the within-subjects variables violation (non-violation, violation) and test item (old, similar), separately for small and large RT savings. The interaction of violation and test item was significant for small RT savings, $F(1, 113) = 3.94$, $p < .05$, $\eta_g^2 = .00$, due to a memory advantage of violated old items over non-violated old items ("old" response rate to old items, non-violation = .64, violation = .67), and the opposite pattern for similar items ("old" response rate to similar items, non-violation = .27, violation = .25). For large RT savings, we did not observe such interaction. All other effects concerning the variable RT savings of the main ANOVA were not significant; four-way interaction, $F(2, 111) = 1.16$, $p > .31$, $\eta_g^2 = .00$, all other $Fs < 1$.

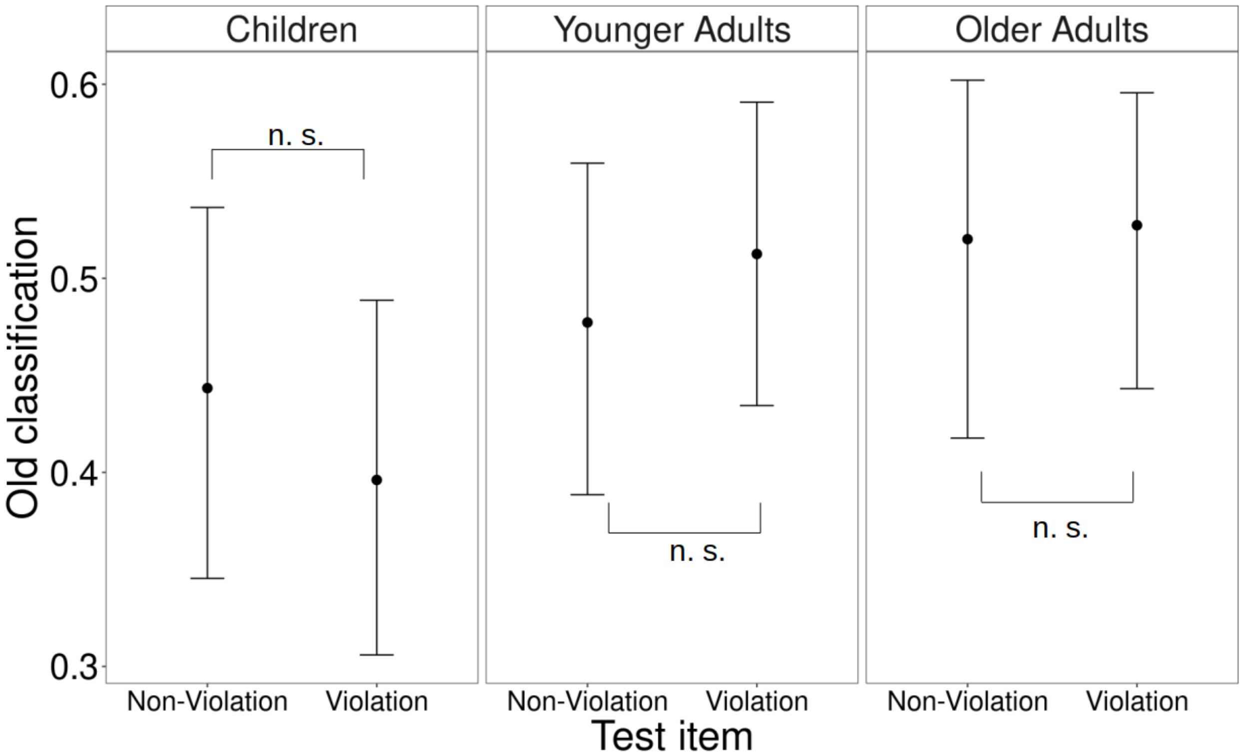
Confusion matrix analysis in the recognition test.

For old items, linear mixed effect models (modeled in lmer function, package lme4 in R) with violation and age group as fixed effects and participant as random effect did not reveal any significant fixed effects, main effect of age group, $\chi^2(2) = 1.44$, $p > .49$, main effect of violation, $\chi^2(1) = 1.71$, $p > .19$, interaction, $\chi^2(2) = 2.78$, $p > .24$ (see Fig. 4.A).

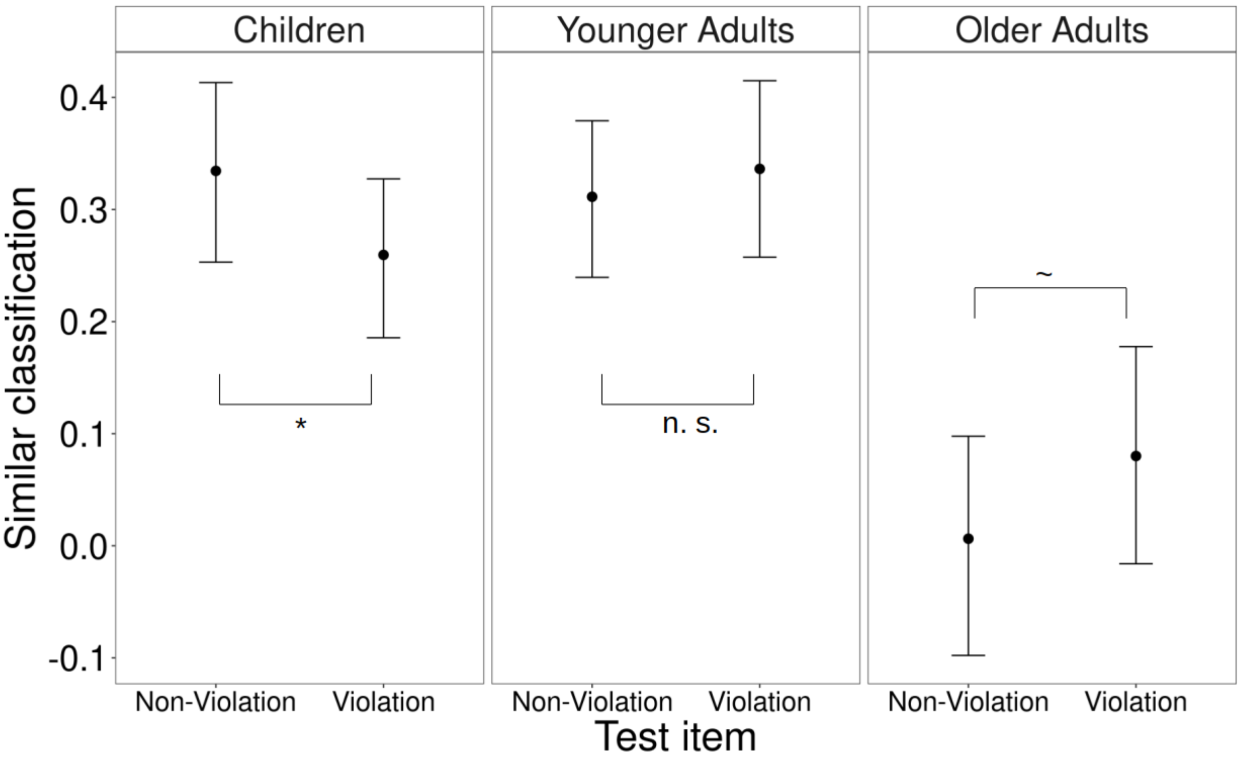
Figure 4

Results of the confusion matrix analysis.

A



B



Note. Error bars depict confidence intervals were calculated based on the method of Cousineau (2005) and Morey (2008).

A. Classification of old items across the different age groups.

B. Classification of similar items across the different age groups. Children show a significant violation effect and older adults are outperformed by both children and younger adults. * ≙ $p < .05$; ~ ≙ $p < .10$; n.s. ≙ non-significant, $p > .1$.

For similar items, the linear mixed effect models with violation and age group as fixed effects and participant as random effect revealed a significant main effect of age group, $\chi^2(2) = 38.21$, $p < .001$, indicating that older adults were outperformed both by children, $\beta = .33$, $t = 5.46$, $p < .001$, and younger adults, $\beta = .31$, $t = 5.18$, $p < .001$. Importantly, the model further revealed a significant main effect of violation, $\chi^2(1) = 3.96$, $p < .04$, and a significant interaction, $\chi^2(2) = 8.44$, $p < .02$. To better understand the violation effect within the different age groups, linear mixed effect models were used with violation as fixed effect and participant as random effect, for each age group separately. The effect of violation was significant in children, $\chi^2(2) = 4.55$, $p < .04$, with better performance for non-violation than violation items. There was no significant violation effect in younger adults, $\chi^2(2) = 0.58$, $p > .44$. In older adults, there was a non-significant trend in the opposite direction, $\chi^2(2) = 3.27$, $p > .07$ (see Fig. 4.B). In other words, children showed better classification for non-violation similar items ($M = .33$) than for violation similar items ($M = .26$), whereas the other age groups did not show this pattern.

Discussion

In the current study, we set out to systematically investigate the effect of PE on episodic memory across the lifespan. Although numerically younger adults did show slightly better memory for violation items, but contrary to our hypothesis, we did not find a significant boosting effect of PE on memory in younger adults, or in any other age groups (children or older adults). Consequently, the expected age-related differences in the PE effect over the lifespan were not observed.

One explanation could be that the PE effect on memory may not be as systematic as previously postulated (Antony et al. 2021; Bein et al., 2021; Brod et al. 2018; Greve et al. 2017; Kafkas & Montaldi, 2018). Indeed, the current results are in line with two recent studies from our lab. In these studies, participants predicted picture categories, and then items from the predicted category or the unpredicted category were shown. None of the experiments revealed a boosting effect of PE on memory (Ortiz-Tudela et al., 2023; Turan et al., 2023). Note that the current study had a methodological advantage of ensuring that the violation and non-violation items differed only in whether they violated participants' predictions about the specific object that was presented. Other factors that influence memory such as item and category novelty, as well as surprise were controlled, since both violation and non-violation items were novel objects (Antony et al., 2021; Frank & Kafkas, 2021). We also made sure not to violate the response participants were made, as the violation item in each pair kept the same response as the predicted item. It is possible that, when controlling for all these additional factors, the effect of PE on episodic memory, in this case derived by violation item-specific predictions, may be rather small and not be observed in all studies.

The strategies we used to isolate the effects of PE from other potential factors described above were also applied in the study of Bein et al. (2021). Of note, there are some differences between that study and the current study that might have led to the difference in results. In our study, participants did the tasks at home due to the COVID 19 pandemic, whereas the study by Bein et al. (2021) took place in the laboratory. We expected somewhat more noise in our data (online data collection may be related to less attention and more distractions for the participants, e.g., Aruguete et al., 2019). Although we did increase power by increasing the sample size in about 30 %, this might not be enough to overcome additional noise. Additionally, we aimed to compensate for these factors by adding more learning blocks and an additional night of sleep for consolidation, hence, in general, an extended learning phase. We did not have any a priori reasons to believe that these differences may attenuate the PE effect. However, consolidation is known to increase semantization and loss of episodic details (e.g., Tompary & Davachi, 2017; Gilboa & Moscovitch, 2021; Moscovitch et al., 2016). Thus, an interesting possibility is that the predictions made were lacking specific item details. Since item-prediction was violated here, this might have yielded different, or less specific, predictions and violations compared to Bein et al. (2021). Other potentially more sensitive measures of PE, such as electroencephalography or eye-tracking, could be used for indices for PE strength that can than more sensitive for in predicting memory performance. Indeed, a recent study using eye-tracking showed that items giving rise to PE were only related to better memory performance when additional changes in pupil dilation occurred during prediction violation (Theobald et al., 2022).

Of all three tested age groups, older adults, contrary to our hypotheses, were the age group that showed the strongest numerical trend for the memory boosting effect of PE. In the descriptive data (response rates), there was a small descriptive trend for a memory advantage of violation over non-violation items, but as in the younger adults, the effect was rather small and cannot be interpreted in favor for the notion of a boosting effect on memory through PE. The confusion matrix analysis corroborates this finding, revealing a slightly stronger, yet non-significant trend, for better memory specificity for violation items than for non-violation items. This rises the question if PE can help older adults counter the decline in memory specificity (by forming more specific memories of items giving rise to PE). While the PE effect was not clearly revealed in older adults, the data showed a strong effect on memory specificity in general. In previous research, older adults have been shown to form fewer specific memories and rely more on gist-like representations, possibly due to a decrease in pattern separation in this age group (e.g., Doxey & Kirwan, 2015; Holden et al., 2013; Stark et al., 2013). Our data consistently showed this effect in all analyses, namely in the relatively high number of similar items being misclassified as "old"; thus, our results nicely align with previous lifespan research.

One interesting, yet unexpected, result was that for children, memory for non-violation items was more specific than for violation items. For non-violation items, children were better able to identify similar lures, and were less likely to confuse similar lures with old items, compared violation items. This effect is in contrast to what has been previously reported in the literature on younger adults. To our knowledge, this is the first time such an effect was reported. It suggests decreased pattern separation for violation items compared to non-violation items in children. It has been argued that PE leads to encoding of distinct memory traces in young adults, such that the events giving rise to PE are remembered separately from previous memory traces (Frank et al., 2020; Gershman et al., 2014; Love et al., 2004). One advantage of such a clear separation of previous memory traces and new memory traces is the avoidance of catastrophic interference, as argued in the complementary learning systems framework (Kumaran et al., 2016; McClelland et al., 1995). Old and new memory traces can thus co-exist and do not necessarily compete. In our children's data, however, the opposite was shown. Together with the absence of a memory boost, this suggests that PE may give rise to conflict that needs to be resolved, and that may restrict encoding of clearly separated memory traces for violations in children compared to adults (see also Brod et al., 2020).

Conclusion

Our objective in this study was to comprehensively examine how PE enhances episodic memory across the lifespan. Unexpectedly, our data did not show that PE was related to significantly better memory in any of the age groups. This finding suggests that PE may not be a strong or consistent modulator of episodic memory after tight control of stimuli properties. The relation of PE and episodic memory encoding may be influenced by further moderators such as individual differences in inhibition, or the nature of the mnemonic representation (detailed, or gist-like). Interestingly, our study provides novel evidence for memory advantages of non-violation items compared to violation items in children for detailed memory, which needs to be replicated and further investigated in future research.

Compliance with ethical standards

The authors declare no conflicts of interest. All procedures were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. Informed consent was obtained from all individual participants included in the study.

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