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Benjamin Tobias Jainta

# The Effects of Encoding, Retrieval, and Modification on Episodic Memory - Neural Substrates and Behavioral Consequences of Prediction Errors

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# The Effects of Encoding, Retrieval, and Modification on Episodic Memory - Neural Substrates and Behavioral Consequences of Prediction Errors

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*Benjamin Tobias Jainta*

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Dekan: Prof. Dr. Gerald Echterhoff

Erste Gutachterin: Prof. Dr. Ricarda I. Schubotz
Zweite Gutachterin: Prof. Dr. Pienie Zwitserlood

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# Summary

Episodic memory is a system that enables the encoding, consolidation, and retrieval of personally experienced events, providing the ability to mentally travel back and forth in time. Since episodic memories are prone to change, recollections of the past are not always accurate representations of experienced events. Conceiving episodic memory as an internal model enabling predictions has offered valuable new perspectives on its prerequisites and functions. In an ever-changing world, prediction errors (PEs) have been identified to serve as learning signals for updating episodic memories when reality contradicts expectations. Thus, the ability to update predictions and to recollect memories in a slightly different way is a necessity for the accurate anticipation of future events. However, research investigating which conditions render episodic memory and how various types of PEs affect the neural mechanisms in the brain is still in its infancy. Therefore, the present thesis aimed to identify the neural substrates and modulating factors of mnemonic PEs and their influence on subsequent episodic memory retrieval.

In order to identify neural and behavioral signatures following the experience of mnemonic PEs in episodic memory, three functional magnetic resonance imaging (fMRI) studies were conducted using a new episodic modification paradigm. First, participants encoded a set of unique, naturalistic episodes from demo videos. In a subsequent fMRI session, subjects were presented with either original or slightly modified versions of the previously encoded episodes. Finally, memory performance was tested through cued retrieval to analyze the impact of PEs on later memory retrieval. In **Study 1**, different agentive states during encoding (self-performance vs. active observation) and perspectives during retrieval (first-person perspective vs. third-person perspective) were used to evaluate the impact of encoding strategies on PE processing and memory performance. **Study 2** examined how

different retrieval practice protocols affect episodic memory stability and, thus, influence brain activity and behavioral performance. **Study 3** aimed to identify distinct neural signatures underlying the experience of repetitive and varying PEs (one single vs. multiple different modified versions).

Across all studies, violating expectations of previously encoded episodes led to increased brain activity during cued episodic memory retrieval. Together, results demonstrated that mnemonic PEs triggered substantial brain responses in the prefrontal cortex (PFC) and superior parietal regions characterized by slightly different episodes, while the anterior cingulate cortex (ACC) was found to indicate strong memory modification effects, i.e., when experienced information differed substantially from an internal model.

**Study 1** revealed that performing rather than only observing an action during encoding subtly modulated hippocampal activity in reaction to mnemonic PEs. Furthermore, the perspective adopted during recall affected the occurrence of false memories, indicating less accurate retrieval from a third-person perspective compared to a first-person perspective. In **Study 2**, PEs elicited a dynamic learning mechanism within brain areas typical for episodic memory reactivation, like the hippocampus, medial frontal, posterior cingulate, and lateral temporal cortices, contributing to recognizing false memories as authentic. Moreover, alterations in retrieval protocols affected brain responses to PEs and subsequent learning. In **Study 3**, repetitive and varying PEs evoked shared and distinct brain activity. Both conditions revealed activation of brain regions typical for detecting mnemonic PEs, like the hippocampus, PFC, and posterior parietal regions. Experiencing multiple different versions of a previously encoded episode resulted in stronger brain responses in hippocampus and caudate nucleus, indicative of the experience of uncertainty, i.e., strong breaches of expectation. Repetitive PEs increased brain activity in cortical midline structures, potentially signaling the successful encoding of an alternative. In line with cortical findings in our study,

varying PEs did not hamper subsequent memory performance, whereas repetitive PEs revealed less accurate recall of original objects.

Beyond demonstrating common neural signatures for repeated encounters of the same PE, repeated mnemonic PEs resulted in subsequent memory modification. While in **Studies 1** and **2** repeated encounters of the same PE were characterized by an increased tendency to form an additional, false memory, **Study 3** showed that repeated, but not varying, PEs impaired cued recall of originally encoded objects. Notably, originally encoded episodes for which no alternative version was presented, led to highly accurate memory performance in all three studies.

Together, these findings offer promising avenues for exploring conditions rendering and mechanisms underlying responses to mnemonic PEs, as well as their impact on episodic memory modification. Experimental data support the view that repeated encounters with the same PE can lead to the encoding of slightly alternative episodes competing with originally encoded information during retrieval. Memory impairments are significantly influenced by the type of PE experienced, yet the impact of self-referential factors and retrieval strategies seems to be rather subtle on episodic memory.

# List of Original Publications

This thesis is based on the following original research articles:

**Study 1** Jainta, B., Siestrup, S., El-Sourani, N., Trempler, I., Wurm M. F., Werning, M., Cheng, S., & Schubotz, R. I. (2022). Seeing what I did (not): Cerebral and behavioral effects of agency and perspective on episodic memory re-activation. *Frontiers in Behavioral Neuroscience, 15*, 793115. https://doi.org/10.3389/fnbeh.2021.793115

**Study 2** Siestrup S., Jainta B., Cheng S., & Schubotz R. I. (2023). Solidity meets surprise: Cerebral and behavioral effects of learning from episodic prediction errors. *Journal of Cognitive Neuroscience*, *35*, 291–313. https://doi.org/10.1162/jocn_a_01948

**Study 3** Jainta, B., Zahedi, A., & Schubotz, R. I. (2024). Same same, but different: Learning from repetitive prediction errors. *Manuscript in press. (Journal of Cognitive Neuroscience*; JOCN-2023-0255.R2).

# 1 Theoretical and Empirical Background

Episodic memory is an essential system driving the ability to encode, store, and retrieve personally experienced information. Therefore, each memory holds a complex interplay of sensory perceptions and contextual details. However, the crux of this cognitive system lies in its imperfection as episodic memories are not always veridical reconstructions of past events (Lee et al., 2017; Nader, 2015; Nader & Einarsson, 2010; Scully & Hupbach, 2020). Despite initially appearing as a flaw in the system, this imperfection serves a functional purpose. Thus, remembering an event in a slightly different version compared to the original experience is a prerequisite for correctly predicting the future (Schacter et al., 2012). In everyday life, the unique nature of events requires our brain to establish a reliable set of regularities while allowing us to adapt to a certain amount of variability and breaches of expectation. A major question deriving from here is: How does the brain utilize correct and/or incorrect predictions to guarantee future predictive success?

Considering episodic memory through the lens of mnemonic PEs offers valuable insights into answering this question. Episodic memory is prone to change, and its gradual modification process is likely driven by retrieval (Lee et al., 2017; Nader, 2015). Recent research on episodic expectations emphasizes the pivotal role of mnemonic PEs during retrieval-induced memory modification (Exton-McGuinness et al., 2015; Fernández et al., 2016). Understanding the process of episodic memory updating requires unpacking the many factors that contribute to learning from PE. Therefore, the present thesis focuses on the neural processing of mnemonic PE and its influence on subsequent memory retrieval to enhance our understanding of the role of PE in memory modification.

The following sections will provide an overview of episodic memory, including the conceptual idea as well as different processes and conditions involved, and explore concepts related to memory modification. Further, this thesis will outline neural substrates of relevant processes and highlight the importance of mnemonic PE as a potential mechanism in memory modification. Finally, relevant findings will be discussed considering the research questions addressed in this thesis.

## 1.1 Episodic Memory – A knowledge-based system

For more than two decades, episodic memory has been widely studied in neuroscience and psychology. As part of declarative memory (Suddendorf & Corballis, 2007; Tulving, 2005), episodic memory was originally introduced to distinguish storage for personally experienced events from general knowledge about the world, i.e., semantic memory (Tulving, 1972). Episodic memories were proposed to be unique in that they jointly include information about the *what, where,* and *when* of a personally experienced event (Tulving, 1972). While it is insufficient to fully distinguish episodic from semantic memory on content alone, the conceptualization has undergone subtle changes over time. For instance, it was suggested that episodic memory retrieval was accompanied by a sense of reliving, termed *autonoetic consciousness* (Gardiner, 2001; Tulving, 1985, 2005). It allows individuals to pick up on significant regularities from the past to project themselves into hypothetical situations, plan future actions, and envision potential outcomes (Tulving, 2002, 2005). Reexperiencing the personal past to predict future events was casually referred to as *mental time travel* (Tulving, 2002). Both reliving past and imagining future events were proposed to share phenomenological characteristics and activate similar brain areas (Suddendorf & Corballis, 2007), appearing as two sides of the same coin. In a highly dynamic world, a system closely linking the past and the future is of great evolutionary benefit.

However, there is no universal consensus regarding the characteristics of episodic memory (Clayton et al., 2003; Conway, 2009; Henke, 2010; Tulving, 2005). For instance, Conway (2009) suggested that episodic memories are defined through the combination of nine different features, like containing sensory-perceptual information, being represented in visual images, and always having a (field or observer) perspective. Henke (2010) postulated three dimensions that differentiate between episodic and other memories: (i) the number of learning trials to correctly memorize, (ii) its level of cognitive complexity, and (iii) the degree of adaptability of the memory. According to these dimensions, Henke (2010) suggested episodic memories to be rapidly encoded and encompass malleable representations. In contrast, semantic memories are believed to undergo gradual encoding and contain rigid representations (Henke, 2010; but see Sharon et al., 2011 for contradictory results). Further, while initial approaches viewed episodic memory as uniquely human (Tulving, 1985), more recent literature has revealed its existence in nonhuman animals (for a review, see Clayton et al., 2003). Across different proposals of episodic memory characteristics, two key features appear to be crucial. First, episodic memory plays an essential role in acquiring new knowledge and transferring it gradually into more general long-term memory. Second, episodic memory provides a basis for adaptive processes that allow planning and goal pursuit (Clayton et al., 2003; Conway, 2009; Henke, 2010; Tulving, 2005).

Episodic memories are suggested to be stored in a representative, rather than a literal, way to allow the mnemonic reconstruction thereof (Cheng & Werning, 2016) by reactivating either individual elements or the whole episode (Henke, 2010). During encounters with new situations, this representational format provides the foundation for the planning and execution of actions and behaviors. To access and reconstruct events from the past, episodic memory relies on the interplay of multiple processes, including encoding, consolidation, and retrieval of experience-based information (Baddeley, 2001, 2004; Tranel & Damasio, 2002). For a better understanding of the different stages in episodic memory formation and subsequent modification, these processes will be described in the following sections.

### 1.1.1 Encoding

To store and later recollect an episodic memory, the content of a personally experienced event must be encoded. Encoding refers to the process through which information is perceived and transformed into a representation that can be stored in the brain. This process involves initial registration and processing of sensory input (Baddeley, 2001, 2004). Several fMRI studies have demonstrated that medial temporal, frontal, and parietal regions are involved in encoding episodic memories (e.g., Manns & Squire, 2002; Shimamura, 2014; Tranel & Damasio, 2002).

Within the medial temporal lobe (MTL), the hippocampus was identified as a core structure of episodic memory (Stachenfeld et al., 2017). Regarding its role in associative learning (Kumaran & Maguire, 2006), the hippocampus creates temporal associations between episodes (Paz et al., 2010), and contributes to the integration of distinct event features (Davachi, 2006; Ranganath, 2010; Rugg et al., 2008; Shimamura, 2014) during encoding. Additionally, MTL supports the binding of coactive features across various areas of the neocortex allowing the creation of similar, but distinct, episodic memories that can be separated from others – a process referred to as *pattern separation* (Norman & O’Reilly, 2003; Yassa & Stark, 2011).

Tightly linked to the hippocampus via bidirectional pathways (Eichenbaum, 2017), the PFC plays another significant role in episodic memory encoding and retrieval. Early neuroimaging studies have revealed the activation of the PFC during both encoding and retrieval of episodic memories (Tulving et al., 1994). While the PFC in general was proposed to be involved in executive control and working memory processes through maintaining information in an active state (E. K. Miller & Cohen, 2001; Shimamura, 2008), the medial PFC (mPFC) was suggested to distinguish memories during encoding of new content to prevent interference (Guise & Shapiro, 2017). Further, the left PFC was found to influence episodic memory encoding (Tulving et al., 1994) by assessing relevant semantic features of an event into an encapsulated episodic memory (Orth et al., 2023; Rugg et al., 2015). Left ventrolateral PFC (vlPFC) was associated with episodic memory encoding (for a review, see Diamond & Levine, 2018). Moreover, neuroimaging studies showing differential prefrontal brain activity during encoding and retrieval formed the basis for the *hemispheric encoding retrieval asymmetry* (HERA) model (e.g., see Habib et al., 2003). According to this model, the left PFC is more strongly associated with memory encoding, while the right PFC is more involved in retrieval (Habib et al., 2003).

Another crucial region for episodic memory encoding was found in the posterior parietal cortex (PPC). Activity in dorsal regions of the PPC was suggested to guide attention toward goal-directed features of an event to facilitate the encoding of attended information (Uncapher & Wagner, 2009). Interestingly, activation of ventral PPC during encoding was proposed to have negative effects on subsequent memory due to its role in reflexive attention, i.e., shifting attention from to-be-encoded information to memory-irrelevant information (Uncapher & Wagner, 2009). In contrast, reduced activity in ventral PPC was suggested to be involved in successful episodic memory encoding (Shimamura, 2011, 2014). Regarding the influence of parietal areas on attentional processes and episodic memory encoding, attention plays a significant role during encoding. Recent research demonstrated that details of events that are more attended during encoding are typically better recalled (Rugg et al., 2015).

### 1.1.2 Consolidation

After the initial learning, memories will undergo stabilization becoming more resilient to disruption by interfering events, a process referred to as *consolidation*. During memory formation, consolidation allows rehearsing knowledge or reactivating events to create a relatively stable memory trace encoded information (McKenzie & Eichenbaum, 2011).

Besides being involved in encoding, it is well-established that the hippocampus takes a crucial role in memory consolidation and closely interacts with neocortical areas (Carr et al., 2011; Dudai, 2004; McKenzie & Eichenbaum, 2011). The hippocampus initiates a process of reactivation and repeated transfer of information between MTL and cortical regions (Squire et al., 2015). Reactivation may occur during active retrieval (Antony et al., 2017; Rowland, 2014) or in periods of non-engagement (Carr et al., 2011; Cheng & Werning, 2013; Tambini & Davachi, 2019). When the brain is not actively processing current events, spontaneous memory reactivation may occur in the hippocampus during awake states (Carr et al., 2011; Tambini & Davachi, 2019) and sleep (Cheng & Werning, 2013) leading to the stabilization and refinement of cortical memory traces.

Early models of memory consolidation, like the *Standard Consolidation Theory* (SCT) (e.g., Squire & Alvarez, 1995), suggested that initial storage of a single memory representation occurs within neocortical-hippocampal connections but undergoes a gradual shift over time toward being solely stored between neocortical connections (reviewed in Simons & Spiers, 2003 and Winocur et al., 2010). This proposal of a gradual shift is in line with the idea that during memory retrieval the mPFC, but not the hippocampus, predominantly mediates the reactivation of episodic memory (Euston et al., 2012). One essential feature of the SCT is that once a memory is consolidated and has become hippocampus-independent, memory becomes immutable (Winocur et al., 2010). However, even stably consolidated memories can regain hippocampal dependence after cueing the experience of previously encoded information and are susceptible to modification (McKenzie & Eichenbaum, 2011).

Over the past decades, various alternative models of memory consolidation have been proposed (for an overview, see McKenzie & Eichenbaum, 2011). For example, the *Multiple Trace Theory* (MTT) proposes a transformation of episodic into semantic memories (Nadel &

Moscovitch, 1997). According to this theory, episodic memories undergo repeated offline reactivations resulting in the integration of common information within cortical semantic networks, thus becoming hippocampal-independent, while episodic information continues to rely on hippocampal-neocortical connections (Nadel & Moscovitch, 1997; Piolino et al., 2009; Winocur et al., 2010). This proposal aligns with neuroimaging studies showing hippocampal activation during retrieval of both recent and remote episodic memories (e.g., Maguire et al., 2001; Ryan et al., 2001). Additionally, the MTT suggests that each time a memory is recalled, it is re-encoded and stored in various cortical regions to form multiple traces or various representations of memory. Allowing encoding of multiple distributed representations, rather than a single engram, is suggested to make memories more resistant to change, but not immutable (Winocur et al., 2010). Although, memories that have undergone extensive consolidation may be less likely modified (Exton-McGuinness et al., 2015; Fernández et al., 2016), reactivating a memory was proposed to return a memory trace into an unstable state, opening a window for modification (Lee et al., 2017; Nader, 2015; Roediger & Butler, 2011).

### 1.1.3 Retrieval

Episodic memory retrieval refers to the recall of a previously encoded event. In the presence of a cue associated with an event, a broad neural network is activated to recollect stored information from medial temporal, frontal, and parietal brain areas (Rugg & Vilberg, 2013; Shimamura, 2014). Over the past decades, an episodic memory core network has been identified including the MTL, PFC, ventral PPC, retrosplenial, and posterior cingulate cortex (pCC) (Jeong et al., 2015; Rugg & Vilberg, 2013).

The MTL is considered to reactivate event features through relational bindings during episodic memory retrieval (Rugg et al., 2015; Rugg & Vilberg, 2013; Shimamura, 2014), referred to as *pattern completion* (Norman & O'Reilly, 2003). In concert with surrounding MTL and neocortical areas, the hippocampus plays a key role in episodic memory reactivation (Jeong et al., 2015; Rugg & Vilberg, 2013; Stachenfeld et al., 2017). Specifically, the hippocampus was suggested to store differential patterns of cortical activity, each representing an ensemble of previously experienced episodic features (Rugg & Vilberg, 2013). Hence, when a suitable retrieval cue is available, the corresponding hippocampal representation is triggered, leading to the reinstatement of the initial pattern of cortical activity and the reexperience of the event (Norman & O'Reilly, 2003). During remembering, hippocampal activity is characteristically accompanied by coactivation in angular gyrus, parahippocampal, retrosplenial, posterior cingulate, and prefrontal cortices (e.g., Rugg et al., 2015).

Regions within the MTL are critical for episodic memory retrieval. However, they must interact with other cortical areas to correctly reactivate sensory, semantic, and other event features. Here, the ventral PPC functions as a central hub that is widely connected with the MTL and PFC as well as sensory regions (Sestieri et al., 2011) and facilitates the coactivation of cortical patterns representing episodic event features (Shimamura, 2014). Further, research suggested dissociable memory functions for dorsal and ventral parts of the PPC based on attentional processes, as proposed by the *Attention to Memory Model* (e.g., Cabeza et al., 2008; Ciaramelli et al., 2008). While the dorsal PPC supports top-down attention processes guiding retrieval goals, the ventral PPC mediates bottom-up attention processes influenced by salient retrieval outputs (Cabeza et al., 2008; Ciaramelli et al., 2008). Moreover, episodic memory retrieval may recruit both medial and lateral regions of the parietal cortex (Cabeza et al., 2008; Henson et al., 1999; Rugg et al., 2015). Within the medial parietal cortex, the precuneus and pCC contribute to visual imagery (Henson et al., 1999;

Rugg et al., 2008). Located in the lateral parietal cortex, the angular gyrus directs attentional resources from retrieval cues to stored content (Cabeza et al., 2008, 2011; Rugg et al., 2015).

Another core structure in episodic memory retrieval is the PFC (see Fletcher & Henson, 2001 and Rugg & Vilberg, 2013 for reviews). Together with the hippocampus, the PFC has been linked to the recollection of contextual information during retrieval (Simons & Spiers, 2003). Early research found the PFC to play an important role in episodic memory encoding, retrieval, and the experience of autonoetic consciousness (Tulving et al., 1994; Wheeler et al., 1997). In line with its role in executive functions and working memory, the PFC contributes to the reactivation of episodic memory features (for a review, see Diamond & Levine, 2018). The dorsomedial portion of the PFC was linked to self-referential processing, an essential part of episodic memory retrieval, whereas the dorsolateral PFC was associated with monitoring episodic memory encoding and retrieval (Brand & Markowitsch, 2008). During retrieval, the vlPFC was suggested to be involved in triggering autobiographical memories and memory selection (Brand & Markowitsch, 2008). The search for the correct representation stored in memory during retrieval is further supported by the mPFC which is activated during retrieval of remote rather than recent memories (Euston et al., 2012). Together with the hippocampus and ACC, mPFC is involved in detecting response conflicts during retrieval (Duncan et al., 2009).

As presented above, episodic memory retrieval is not merely a passive recollection of past events, but rather a dynamic phenomenon influenced by different brain areas with various functions. Therefore, the ability to retrieve memories allows access to a stored representation for future planning and goal pursuit but further opens a window to encoding new, diverging information (Conway, 2009). Therefore, episodic retrieval serves one of the most important aspects of human memory: memory modification.

## 1.2 Episodic Memory Modification

Despite the strong tendency to perceive episodic memory as a faithful and stable reflection of past events, mnemonic representations are rather dynamic and prone to change (Lee et al., 2017; Nader, 2015). Thus, it is suggested that episodic memory underlies a reconstructive process rather than mere retrieval of memory traces (e.g., Cheng et al., 2016). The following sections will describe concepts reflecting the constructive nature of memories as well as different types of memory modification to provide a conceptual idea of how episodic memory can be updated.

### 1.2.1 Imagining is (not) Remembering

Early research reported that amnesic patients have problems with imagining the future suggesting a lack of the ability to mentally travel back and forth in time (Klein et al., 2002; Tulving, 1985). Since then, numerous findings from psychology and cognitive neuroscience have suggested a close interaction between past and future thinking while sharing similarities with imagining events (e.g., Hassabis et al., 2007 and Okuda et al., 2003; or see Schacter et al., 2012 for a review).

Imagination has been linked to mentally simulating novel experiences (Hassabis, Kumaran, & Maguire, 2007; Hassabis, Kumaran, Vann, et al., 2007), planning future events, and remembering the actual past (Addis et al., 2007; de Vito et al., 2012; Szpunar et al., 2007). Neuroimaging studies identified a common network for thinking of the future and remembering the past (Hassabis, Kumaran, & Maguire, 2007; Okuda et al., 2003) leading to the conclusion that episodic memory contributes to imagining future events (Addis et al., 2007). Further, imagining the future and remembering the past were found to activate similar brain networks including frontal, posterior cingulate, retrosplenial, and lateral parietal cortices, as well as the MTL (Schacter et al., 2012; Szpunar et al., 2007). Interestingly, the hippocampus was suggested to play a crucial integrative role during imagination and episodic memory as both systems are associated with constructive processes (Hassabis & Maguire, 2007, 2009). Further, imagination was suggested to lead to vivid mental projections of oneself in future events (Szpunar et al., 2007), especially when thinking of familiar (rather than unfamiliar) settings and self-relevant (than self-irrelevant) events (de Vito et al., 2012). Additionally, it was shown that both imagining the future and remembering the past are prone to the effects of aging. When imagining the future or remembering the past, healthy older adults provide less detailed episodic descriptions than young adults which may result from changes in episodic memory mechanisms (see Schacter et al., 2013, for a review).

This intricate interplay between imagination and episodic memory raises the question of whether the mind can construct mnemonic representations that feel real but diverge from actual past experiences. Concerning our imperfect memory system, the simple answer is: yes.

### 1.2.2 Constructing Episodes

In recent years, episodic memory has increasingly been considered a constructive, rather than reproductive, process (Schacter & Addis, 2007). It was suggested that episodic memory does not simply make available a stored representation but collects various stored information associated with an event to reconstruct it during retrieval (Cheng et al., 2016). This perspective is in line with research suggesting that memory features are distributed widely across different brain areas (e.g., Cabeza & St Jacques, 2007) and are recombined during pattern completion to comprise a specific past event (Norman & O’Reilly, 2003).

To provide accurate representations of the past, a constructive memory system must solve many problems. For example, episode features must be bound together during encoding to prevent later source memory failure, i.e., misattributing the origin or context of a memory, leading to inaccurate recall of where, when, or how information was encountered (Schacter, 1999). In order to correctly remember, selective recall is necessary to distinguish one memory from another during retrieval (Schacter, 1999). A key region mediating this selective retrieval process is the PFC (Schacter & Addis, 2007). Patients with damage to prefrontal regions were found to vividly remember events that never happened (see Schacter & Addis, 2007, for a review). Nonetheless, even healthy people tend to falsely recall events that were never experienced in the first place, like after suggestion, mere convincing (Lindsay & Read, 1994; Loftus & Pickrell, 1995; Schacter, 1999), or false information (Mangiulli et al., 2022). In line with this susceptibility, it was suggested that constructive processes may be biased by individual beliefs, perspectives, semantic knowledge, and prevailing circumstances (Schacter et al., 2012), or limited by working memory capacity (Cheng et al., 2016). Further, Cheng et al. (2016) proposed that constructing scenarios from episodic memory is deeply connected to other cognitive and memory systems.

While encountering numerous challenges during the reconstruction of the personal past, recollecting accurate memories appears rare. A recent proposal suggested that constructing memories reflects the attempt to make sense of the world while potentially sacrificing the veridicality of memories and in part creating false memories (Conway & Loveday, 2015). Although this reconstructive nature of episodic memory may appear as a flaw in the system, it rather serves an adaptive role. In a highly complex, constantly changing environment a mere reproduction of stored memories would rather be useless for future events. Therefore, it is important to understand how and when new information is incorporated into memory while updating old or forming new (false) memories.

### 1.2.3 False Memory Formation

Memory is an adaptive system supporting the encoding and retrieval of different information. Therefore, it is not surprising that major or minor confusion may occur creating false memories. For example, repeated imagination of an event that has never happened may increase the tendency to remember it as actually experienced. The phenomenon causing an illusory memory has been labeled *imagination inflation* (for a review, see Schacter et al., 2011). Studies showed that simply imagining an event that supposedly occurred in the past (when in fact it did not) can inflate the confidence to have experienced this fictitious event (Garry et al., 1996). Creating false memories may result from perceptual and conceptual features of previously experienced events misattributed to the imagined event (Schacter et al., 2011). Early studies of memory distortion provided further evidence for false memory formation (Brainerd & Reyna, 1998; Loftus, 1997; Loftus & Pickrell, 1995). Repeated exposure to a childhood event (without direct experience) led participants to falsely remember this event as truly experienced by them (Loftus & Pickrell, 1995; Wade et al., 2002). Further, using different techniques during interviews (e.g., guided imagination or suggestive questioning) can lead to the creation of false memories (Lindsay & Read, 1994; Loftus & Pickrell, 1995; Schacter, 1999). Therefore, while aiming for more accurate recall, suggestive techniques may result in the unexpected consequence of leading people to misremember.

False memory formation does not exclusively emerge from external suggestion. Encountering new post-event information can result in erroneous acceptance of misleading information or false rejection of actual events, a phenomenon referred to as the *misinformation effect* (Loftus, 1991, 2005). Further, when individuals learn two distinct sets of information (such as lists of words or objects), information belonging to the second set may be falsely remembered as originating from the first set. Typically, this *memory intrusion* is asymmetrical as the first is usually observed to be less likely to intrude on the second set (e.g., Hupbach et al., 2007, 2009). Additionally, *false recognition* can occur when a novel event is mistakenly identified as previously encountered, frequently resulting from high similarity between precepted and stored information (Schacter, 1999).

Together with the constructive nature of episodes, false memory formation sheds light on the phenomenon that new information may be accidentally integrated into existing memories. In the following section, a commonly accepted process of information integration into memory will be presented in detail.

### 1.2.4 Reconsolidation

A groundbreaking study by Nader et al. (2000) challenged prevailing beliefs that memories undergo an immutable stabilization through a cellular consolidation process that takes place only once, shortly after initial learning (for a review, see Davis & Squire, 1984). Nader et al. (2000) demonstrated that retrieval of a pre-existing fear memory puts it in an unstable state requiring additional protein synthesis to restore the memory. Supported by additional research (e.g., Kida et al., 2002; Sara, 2000), this finding implies that memory reactivation opens a temporal window for *reconsolidation*, a process that returns a consolidated memory to a labile and modifiable state (referred to as *destabilization*) followed by a period of re-stabilization (Lee et al., 2017; Nader, 2015).

Once put in a labile state, memories can be modified in different ways such as updating existing with new information and strengthening or weakening the original memory trace (for reviews, see Finn, 2017 and Haubrich et al., 2020). For instance, blocking the protein synthesis shortly after reactivation was shown to weaken (or even erase) the original fear memory (e.g., Nader et al., 2000). Reconsolidation is vulnerable to many of the same interventions as consolidation, like presenting interfering information after reactivation, using electroconvulsive shocks, or applying protein synthesis inhibitors (Lee et al., 2017). Further, reconsolidation was described as a time-dependent process that can occur within hours after reactivation due to new protein synthesis (Elsey et al., 2018; Kiley & Parks, 2022; Lee et al., 2017). Additionally, behavioral interventions have the potential to induce memory modification throughout the reconsolidation window. For instance, in case of emotional memories, extinction learning after reactivation of a conditioned stimulus was demonstrated to potentially lead to a lasting decrease in the conditioned reaction (e.g., Monfils et al., 2009). As mentioned in the previous section, reactivation of a previously learned list of words followed by a second list can lead to memory interference during later recall of the original set (e.g., Hupbach et al., 2007). Over the past two decades, research conducted in both animals and humans has provided substantial evidence in favor of the reconsolidation theory for different types of memories (Hupbach et al., 2007; Monfils et al., 2009; Nader et al., 2000; Sinclair & Barense, 2018).

While in animal research, pharmacological treatments have been typically used as proof of reconsolidation through the incorporation of new information and strengthening or weakening of the original memory, this method is difficult to apply in research on humans due to its invasive nature (Schiller & Phelps, 2011). Therefore, non-invasive techniques like extinction learning (e.g., Schiller et al., 2010) or memory interference paradigms (e.g., Hupbach et al., 2007) were mainly used to investigate reconsolidation-based memory updating in humans (see Schiller & Phelps, 2011, for a review). Behavioral interventions emphasize the temporal dependency of reconsolidation as interference appears most effective with longer periods between encoding, reactivation, and subsequent testing of original memories (e.g., Hupbach et al., 2007; Sinclair & Barense, 2018). Conversely, behavioral interventions targeting consolidated procedural memory indicate that interference does not impair subsequent recollection in the context of short-term memory (i.e., when reconsolidation is not completed) (Walker et al., 2003).

Despite the numerous studies supporting the reconsolidation theory (for a review, see Elsey et al., 2018), the field of human reconsolidation research still faces several challenges as mixed findings and failed replications demonstrate that the current understanding is not as straight-forward as the reconsolidation theory proposes (e.g., Gisquet-Verrier & Riccio, 2012; Hardwicke et al., 2016; Klingmüller et al., 2017; Levy et al., 2018). A recent review by Gisquet-Verrier & Riccio (2018) proposed a *memory integration concept* suggesting that memory modification results from changes in the internal state of the subject, rather than external information, resulting in rapid updating of a malleable memory trace after reactivation. Thus, results supporting the traditional reconsolidation view may reflect state-dependent effects rather than memory reconsolidation (for a detailed discussion, see Gisquet-Verrier & Riccio, 2018). Further, it was argued that many findings supporting the reconsolidation theory originate from various memory systems, often investigated through different paradigms (Gisquet-Verrier & Riccio, 2018). Consequently, it is essential to identify potential interactions between them(Schiller & Phelps, 2011).

Although reconsolidation theory alone may not fully account for the multifaceted mechanisms in memory modification, it highlights two important functions: (i) the updating of old memories with new information and (ii) strengthening (or weakening) the original memory (Lee et al., 2017; Nader & Einarsson, 2010) to maintain their relevance and stability in everyday life (Lee, 2009).

It has been proposed that the mnemonic strength of a reactivated memory and the experience of a mismatch between expectation and actual experience are two determinants of whether a memory would destabilize and subsequently be modified or not (Fernández et al., 2016; Pedreira et al., 2004). To better account for these key determinants, the following sections will first briefly describe two factors potentially rendering episodic memory and, second, highlight the pivotal role of mnemonic PEs.

## 1.3 Conditions Rendering Episodic Memory

### 1.3.1 Visual Perspective

As episodic memories are not always precise recordings of events, they rather represent the unique point-of-view that one has from self-performed or observed actions. Visual perspective is a flexible and dynamic property attributed to the inherent nature of memories (Harris et al., 2015; Robinson & Swanson, 1993). Events may be initially experienced and later retrieved from a field or first-person perspective (1pp) or an observer or third-person perspective (3pp) (Nigro & Neisser, 1983; Robinson & Swanson, 1993). In everyday life, these perspectives are naturally based on whether we are self-performing (from 1pp) or only observing (from 3pp) an action[1].

First-person perspective has been referred to as the default during episodic memory encoding (St. Jacques, 2019), but constructive processes during the initial experience of an event may affect subsequent memory retrieval and lead to multiple viewpoints for a single event (Nigro & Neisser, 1983; St. Jacques, 2024). Pre-setting the encoding perspective through a video-based out-of-body experience (i.e., 3pp) was reported to decrease activity in the left posterior hippocampus during later retrieval and reduce memory accuracy and vividness (Bergouignan et al., 2014). Further, the perspective one takes during encoding affects the spontaneously adopted perspective during recall (Bergouignan et al., 2022).

Episodic memories predominantly remembered from 1pp compared to 3pp were found to be recalled more accurately and more vividly (Marcotti & St. Jacques, 2018; Rice & Rubin, 2009). However, the perspective adopted during retrieval may diverge from the one experienced during the initial event. Regarding memory retrieval, a natural shift from 1pp to

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[1] There is one exception in daily life, where naturally a 1pp is adopted while observing another person's action, i.e., when people are teaching children certain movements while sitting behind them and putting their arms around them to assist. Due to its rare appearance in action observation, this setting will not be further discussed in this thesis.

3pp was observed for more remote than recent memories (Nigro & Neisser, 1983; Rice & Rubin, 2009) and may lead to less accurate memory due to a loss of visual information (Janssen et al., 2011). Repeated retrieval from 1pp may slow this natural shift, and thus, is associated with retaining visual information of memories whereas a repeated recollection from 3pp rather leads to loss thereof (Butler et al., 2016). Moreover, an active shift from 1pp to 3pp during memory retrieval is associated with less accurate memory recollection (Marcotti & St. Jacques, 2018). Even though shifting back from 3pp to 1pp does not recover the loss of visual information (Butler et al., 2016), it may increase the number of episodic details about the self during reports (e.g., King et al., 2022). The ability to shift visual perspective during retrieval was suggested to potentially subserve updating processes (St. Jacques, 2019).

Distinct neural mechanisms have been identified to support memory retrieval from a 1pp or 3pp (Eich et al., 2009; Gauthier et al., 2020; St. Jacques, 2019, 2024; Vogeley & Fink, 2003). Both 1pp and 3pp have been associated with the engagement of the medial parietal cortex, including the precuneus, during memory retrieval (St. Jacques, 2019). Specifically, the precuneus and angular gyrus were found to be involved in the ability to actively shift visual perspectives during memory retrieval and, consequently, reshaping memories (St. Jacques, 2019; St. Jacques et al., 2017). Neuroimaging studies suggest that taking a 1pp (compared to 3pp) during memory is associated with brain regions mediating interoceptive and self-referencing processes, for example, leading to increased activity in the amygdala and decreased activity in the insula and sensory-motor cortices. In contrast, adopting a 3pp rather than 1pp triggers stronger decreases of activity in brain regions associated with interoceptive awareness (e.g., Eich et al., 2009; but also see Grol et al., 2017). Taking a 3pp during retrieval was further associated with greater engagement of the temporal parietal junction (St. Jacques, 2019), a core region in theory of mind processes, representations of the bodily self, and action observation (Blanke, 2012; Spreng et al., 2009; Yang et al., 2015).

Interestingly, several reviews highlighted a close link between episodic memory retrieval and visual imagery due to sharing (re-)constructional properties (Rubin, 2005; St. Jacques, 2019, 2024; Vogeley & Fink, 2003). For example, Ruby & Decety (2001) reported increased activity in left inferior parietal lobe and somatosensory cortex during 1pp were considered to reflect the planning and visualization of actions. In contrast, activation of the right inferior parietal cortex was found during 3pp and associated with imagining a third person in action (Ruby & Decety, 2001).

Understanding the role of visual perspective in episodic memory may be of great benefit as it not only influences how events are remembered but further shapes the accuracy and subjective experience during recollection. However, visual perspective is naturally confounded with the agentive state a person took during the experience of an event. Therefore, the next section will review findings from research on agency.

### 1.3.2 Agency

Regarding encoding information, many people assume that learning by doing is better than learning by observing. Accordingly, a large body of literature suggests that self-performed tasks are remembered more accurately than tasks that have been only verbally described or tasks performed by an experimenter (for reviews, see Engelkamp, 2001 and Engelkamp & Dehn, 2000).

In memory paradigms, the advantage of learning by doing is referred to as the *enactment effect* (Roberts et al., 2022). This effect relates to the phenomenon that self-performance compared to sole observation (or reading about an event) leads to superior memory performance during subsequent retrieval (Roberts et al., 2022). Early studies investigating the enactment effect showed that performing an action described by a word or phrase resulted in better memory performance and more vivid recall than reading about, imagining, or observing the related action (Engelkamp & Krumnacker, 1980; Engelkamp & Zimmer, 1984; Hornstein & Mulligan, 2001; Mulligan & Hornstein, 2003; Senkfor et al., 2002). On a neural basis, performed actions compared to interrupted (Leynes et al., 2005) or non-performed actions (Leynes et al., 2006; Senkfor et al., 2002) elicit differential activity patterns. Enhanced event-related brain potentials were found in parietal regions suggesting a selective recollection of sensorimotor information for previously self-performed actions (Leynes et al., 2005, 2006; Senkfor et al., 2002). Further, neuroimaging studies showed that retrieval of previously self-performed compared to verbally encoded actions elicits activity in pre-motor and primary motor cortices, as well as supramarginal gyrus (SMG) during retrieval (Krönke et al., 2013; Nyberg et al., 2001; Russ et al., 2003). Russ et al. (2003) argued that SMG activation indicates the binding of object knowledge and motor planning into a coherent action representation. Although the benefit resulting from self-performed actions appears to be highly robust, especially when compared to verbally described actions, it is not always superior to actively observing actions (Steffens, 2007).

The abovementioned studies investigated the enactment effect using very simple actions like ‘knock on the door’ (e.g., Mulligan & Hornstein, 2003). In more complex sequence learning tasks, the expected beneficial effect of enactment did not translate to later testing (e.g., Boutin et al., 2010). Further, the enactment effect may depend on whether the encoded information is semantically related to the performed action or not (Sivashankar & Fernandes, 2022) as only observing others performing meaningful actions can already improve later memory performance (Sivashankar et al., 2023). Therefore, it remains an open question whether or not the enactment effect influences encoding and subsequent retrieval of more complex actions or events typical for episodic memory.

## 1.4 The Role of Predictions in Episodic Memory

### 1.4.1 Predictive Coding Theory

In an ever-changing world, the brain's ability to predict future events provides an evolutionary advantage that may have resulted in the development of episodic memory (Suddendorf & Corballis, 2007). Consequently, the interplay between prediction and episodic memory has raised major interest in the field of cognitive neuroscience (Mullally & Maguire, 2014).

An appealing framework explaining how the brain understands and predicts future events and actions is the *Predictive Coding Theory* (Clark, 2013). This theory states that by generating an internal model of the world, the brain estimates the state of the world before receiving perceptual input. It was proposed that these generative internal models are probabilistic in nature as they depend on statistical regularities emerging from the environment (Clark, 2013, 2015; Friston, 2003). To successfully predict a dynamically changing world, the internal model was suggested to follow Bayesian inference (see Friston, 2010 or Knill & Pouget, 2004, for a detailed description). Through top-down connections within a hierarchical multilevel system, encoded sensory data are used to predict the most probable sensory input and related events. Predictive capabilities improve with learning through bottom-up signals adapting and updating internal models (Friston, 2003, 2010). Thus, the brain continuously compares predicted with actual perceptual input while detecting discrepancies or mismatches between the internal model and the world (Clark, 2013, 2015). This mechanism allows the brain to efficiently reduce the amount of uninformative, i.e., correctly predicted, sensory data and to focus on the processing of informative, i.e., unpredicted, new information (Friston, 2003, 2005; Sayood, 2018). The difference between experience and expectation is most referred to as 'prediction error' (PE) and leads to optimizing the neural processing of diverging information and internal model updating (Clark, 2013; Friston, 2005; Sayood, 2018).

PEs may be seen as the main driving force in a bidirectional learning cascade of a hierarchical multilevel system. In this system, predictions are conveyed via backward connections from higher processing areas to lower sensory regions (top-down), while PEs are typically transmitted through forward connections, facilitating the propagation of PEs from lower to higher levels (bottom-up) (Clark, 2013; Friston, 2003). Thus, top-down signals aim to minimize PEs, reflecting what an internal model or system already knows about the world, whereas bottom-up signals provide access to information that needs to be learned, leading to efficient encoding (Clark, 2013).

However, learning from PE may vary due to the type of unexpected information. Regarding perceptual and cognitive processes, PE reflects the degree of surprise with respect to a particular outcome. Perceptual PE detection has been associated with increased activation of visual and auditory areas, while cognitive PE detection was identified in prefrontal regions responding to abstract rule violations (den Ouden et al., 2012). When focusing on motivational aspects, PE rather indicates the valence of an outcome, i.e., whether it was better or worse than expected. In reinforcement learning paradigms, motivational PEs have been found to mediate activity in the striatum, amygdala, and ventral tegmental area, reflecting a strong link to dopamine circuits (den Ouden et al., 2012). At first glance, it may appear that a cortical-subcortical division may exist regarding the type of PE but in fact, this is not the case (see den Ouden et al., 2012, for a review).

In general, PE has been proposed to signal salience and attract attention through information that stands out from well-learned regularities guiding the selection of actions and goals (den Ouden et al., 2012; Diederen & Fletcher, 2021). Although playing a crucial role in learning, PE detection alone does not guarantee internal model updating. For updating, it is important how ‘reliable’ or ‘precise’ a prediction was and whether the predicted information failed to match the sensory inputs due to content (e.g., we look for our car in a parking area, but our car is missing) or due to noise (e.g., we look for our car, but the other cars around changed) (den Ouden et al., 2012; Friston, 2005). Therefore, understanding how and why a piece of information is surprising is crucial for comprehending its updating mechanisms.

In recent years, the concept of predictive coding, and therefore the processing of PE, has been linked to episodic memory (e.g., Barron et al., 2020; Fountas et al., 2022). In contrast to real-time processing of PEs during sensory perception, memory recall was suggested to generate hypothetical ‘offline’ PEs allowing the brain to prepare for future sensory input (Barron et al., 2020). Further, successful and violated predictions have repeatedly been shown to affect memory outcomes (e.g., Pupillo et al., 2023). Thus, the following sections will outline the effects and neural substrates of mnemonic PEs on episodic memory.

### 1.4.2 Mnemonic Prediction Errors

In several studies, PEs have been identified to encode new and/or shape existing episodic memories (e.g., Pupillo et al., 2023; Sinclair & Barense, 2018). Additionally, PEs were suggested to initialize the encoding of new information by experiencing unexpected changes within an originally learned event or by encountering new events[2] similar to previously encoded ones (Henson & Gagnepain, 2010; Krawczyk et al., 2017). Therefore, irrespective of whether creating new or modifying existing memories (Krawczyk et al., 2017),

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[2] Following the predictive coding approach (cf. section 1.4.1), the brain may be seen as a predictive machine, generating expectations for every newly encountered scenario or event. Some authors distinguish between a state of ‘absolute novelty’ and ‘contextual novelty’ (Kafkas & Montaldi, 2018b). Absolute novelty arises from weak expectations, when an event is completely new and expectations about what is likely to occur are low, resulting in learning a novel event. In contrast, contextual novelty reflects a state that allows specific expectations with respect to a given context initiating learning due to slightly different details in an event (Kafkas & Montaldi, 2018b). However, if perceptual input is too different from previously experienced events, this is usually referred to as new learning rather than PE-based updating of original memories (Milton et al., 2023).

PE mechanisms appear beneficial in light of an ever-changing world (Sinclair & Barense, 2019).

New experiences trigger the reactivation of an original memory and, thus, enable memory updating and subsequent reconsolidation to ensure their relevance in a dynamically changing environment (cf. section 1.2.4). Reactivating a memory opens a window to either strengthen or weaken the stored memory (Lee et al., 2017). PE has been suggested to play a major role in how reactivating an original memory can lead to subsequent modification (Pedreira et al., 2004; Sevenster et al., 2014). Interestingly, many studies have used incomplete reminders (i.e., interrupting retrieval of an episode) to trigger PEs during episodic retrieval (see Sinclair & Barense, 2019, for a review). Incomplete reminders of an episode have been demonstrated to reactivate an original memory making it susceptible to subsequent modification (Hupbach et al., 2007; Sinclair & Barense, 2018). When followed by complete retrieval, incomplete reminders were suggested to promote long-term memory retention (Antony et al., 2017). Therefore, reactivation through incomplete reminders can distort, strengthen, or update memories depending on whether the reminder was followed by competing information or not (Sinclair & Barense, 2019). Importantly, an effective reminder provokes a PE signal to facilitate updating through destabilization and subsequent re-stabilization (Fernández et al., 2016).

However, not all PEs affect memory modification in the same way. It was suggested that strong PEs occur when an unexpected stimulus is encountered, for instance, a novel item in a familiar context or a familiar item in a novel context. In both cases, the brain fails to correctly predict the item and/or context, leading to a large PE in the system and a need to encode new information (Henson & Gagnepain, 2010). Recent studies showed that failed predictions may (but not always will) be remembered better than successful predictions (Brod et al., 2020; Greve et al., 2017; Kafkas & Montaldi, 2018a; Quent et al., 2022). In contrast, weak (or no) PEs resulting from successful predictions in response to a stimulus were proposed to lead to less impactful changes in a memory system and, thus, less successful encoding than stronger PEs (Henson & Gagnepain, 2010). However, well-predicted events (weak PE) can also lead to better subsequent memory retrieval, i.e., when an event is congruent with a person's knowledge. Such a *memory congruency effect* has been observed in multiple studies (Bein et al., 2015; Brod & Shing, 2019; Ortiz-Tudela et al., 2017). These effects on subsequent memory retrieval may result from a shift of attention toward unexpected, new information (Bein et al., 2021; Wahlheim & Zacks, 2019) or, in case of congruent knowledge, a more elaborative encoding thereof (e.g., Bein et al., 2014). Models focusing on congruency effects and knowledge integration propose that the relationship between PE and memory performance may be described by a U-shaped function (Van Kesteren et al., 2012). Thus, only extreme, but not intermediate, levels of PE would predict better memory performance. However, there has been research showing better memory performance after experiencing intermediate compared to extreme levels of PE (e.g., Ortiz-Tudela et al., 2023).

The influence of PE on memory modification appears multifaceted. In general, PE can alter later memory retrieval in different ways and offers insights into how new information may be integrated into existing memories. As memory reactivation through PE is an effective tool for modification, the following section will take a closer look at the neural substrates underlying this interplay.

### 1.4.3 Neural Substrates of Detecting Mnemonic Prediction Errors

Predictive coding proposes that neural activity is orchestrated in order to minimize PEs, aiming for a fully predicted representation of the environment (Clark, 2013). Although it is useful to store and retrieve events that are consistent with our expectations, the brain must identify those that violate them. As a core structure of episodic memory, the hippocampus is taken to be essentially predictive (Stachenfeld et al., 2017), contributing to associative learning and generating associative predictions (Bein et al., 2020; Duncan et al., 2012; Kumaran & Maguire, 2006, 2007; Long et al., 2016; Schlichting et al., 2015) underlining its pivotal role in mismatch detection (Chen et al., 2011; Duncan et al., 2009; Kumaran & Maguire, 2007). Therefore, the hippocampus mediates comparisons between newly experienced information and stored representations, leading to memory updating (e.g., Duncan et al., 2009; Kumaran & Maguire, 2007; Long et al., 2016). Moreover, hippocampal activation was found to be indicative of the formation of false memories after experiencing PEs (Sinclair et al., 2021).

However, as the brain was suggested to process and examine a large quantity of semantic and episodic information while experiencing complex events (for a short review, see Schubotz, 2015), the hippocampus alone cannot sufficiently provide predictive signals and process mismatch detection. Although still in its infancy, an increasing body of research identified brain regions beyond the hippocampus to be involved in detecting mismatches and mediating PEs in complex events (e.g., Hrkać et al., 2015; Schiffer & Schubotz, 2011; Wurm & Schubotz, 2012). For instance, the PFC was found to detect mismatches in complex scenarios, while activity in ACC reflects a need to adapt expectations based on experienced PE (Schiffer & Schubotz, 2011). In line with the idea that the brain explains away PEs by encoding new information (Barron et al., 2020), the mPFC was found to be involved in mismatch detection and the integration of new information (Garrido et al., 2015; Van Kesteren et al., 2012). Further, the caudate nucleus was repeatedly identified to respond to breaches of expectation (e.g., Delgado et al., 2008; Schiffer et al., 2012; Schiffer & Schubotz, 2011).

According to predictive coding theory (e.g., Barron et al., 2020; Clark, 2013), it is of tremendous importance to adapt an internal model to persistent changes and maintain valid predictions. The amount of brain activity and thus model adaptation were reported to depend on the solidity of an internal model (Schiffer et al., 2012, 2013). Research on complex events revealed attenuating activity in a frontoparietal network (Schiffer et al., 2013), the substantia nigra, and the hippocampus (Schiffer et al., 2012) in response to repeated presentation of the same unexpected, mismatching information. Moreover, solid compared to weak internal models triggered increased brain activity in the parahippocampal gyrus (Schiffer et al., 2013).

While the role of PEs in memory has been extensively studied behaviorally (c.f. 1.4.2), the underlying neural mechanisms are far from being fully understood. Most imaging studies focused on rather simple or static stimuli, like the presentation of word or object pairs (e.g., Chen et al., 2011; Duncan et al., 2009; Long et al., 2016), or contextual scenes (e.g., Bein et al., 2020; Duncan et al., 2012; Ortiz-Tudela et al., 2017). In real-life situations, complex events are unfolding over time which static images of scenes and objects may not account for. A series of studies demonstrated how mnemonic PEs affect brain activity depending on action observation, as well as semantic and episodic information (Schiffer et al., 2012, 2013; Schubotz et al., 2014; Wurm et al., 2014). However, these studies did not investigate the influence of learning from PEs on subsequent memory performance, potentially resulting in strengthening or weakening of true, or formation of false memories. Yet, only a few studies inspected the effects of mnemonic PEs during the experience of complex stimuli (i.e., episodic videos) (Sinclair et al., 2021; Sinclair & Barense, 2018). Against this background, more research is necessary to understand how mnemonic PEs affect brain and behavior.

# 2 Research Questions and Objectives

As highlighted in the sections above, episodic memory is the ability to encode and later retrieve experiences to predict future events. These memories shape how we see ourselves and the world surrounding us. However, episodic memory does not function like a recorded tape that can be replayed repeatedly in the exact same way. Especially, when reality violates our expectations, episodic memory must be updated to adapt to and survive in an ever-changing world. Emerging from the predictive coding theory, one driving force behind this updating process was found to be PE. Investigating this multifaceted process allows us to better understand the neural mechanisms behind episodic memory and its impact on behavioral outcomes.

The study of neural processing and behavioral outcomes of PEs still faces many challenges due to the use of various types of stimuli and PEs that do not always fully capture the complexity of episodic memory. Therefore, the current thesis examined how more naturalistic PEs amplify brain activity and hamper memory retrieval. Moreover, the evidence provided above highlights the role of hippocampal and prefrontal areas in episodic memory and signaling mnemonic PEs. To investigate which conditions render episodic memory and which neural substrates underly the processing of mnemonic PEs, the following specific research questions were addressed in three fMRI studies, respectively:

1. What influence do variations in agentive states during encoding and perspectives during retrieval have on responses to mnemonic PEs and episodic memory modification?

2. What impact do different memory consolidation strategies have on the neural processing of mnemonic PEs and subsequent memory performance?

3. How do different types of mnemonic PEs affect neural responses underlying learning from PEs in episodic memory?

A series of two pilot and three fMRI studies was conducted to answer the targeted research question. To this end, a previously developed episodic modification paradigm was adapted (Schiffer et al., 2012, 2013). Two pilot studies were conducted to develop a set of unique action videos (in the following referred to as *episodes*) and to establish a suitable encoding procedure. In all three fMRI studies, participants encoded episodes by either self-performing or actively observing demo videos showing toy stories. In **Study 1**, half of the episodes were imitated while the other half was actively observed, whereas episodes were only self-performed in **Study 2** and only observed in **Study 3**. In a subsequent fMRI session, subjects were either presented with previously encoded episodes or slightly modified versions thereof. Modified episodes were used to trigger mnemonic PEs. Finally, subjects conducted a behavioral memory test.

**Study 1** investigated how agency during encoding and perspective during retrieval affect neural processing of mnemonic PEs and subsequent memory performance. In general, modified episodes were expected to elicit substantial brain activation in areas engaged in mnemonic PEs. Further, it was hypothesized that (i) encoding by self-performance rather than mere observation and (ii) retrieval from a 1pp compared to 3pp would lead to (a) stronger brain responses during expectation violation and (b) more accurate memory performance during post-fMRI testing.

**Study 2** examined how different consolidation protocols influence episodic memory stability in brain and behavior. Additionally, **Study 2** investigated dynamic brain responses that contribute to the emergence of subsequent false memories. Consequently, fMRI data for modified episodes was analyzed regarding false alarms and correct rejections in the memory test. It was expected that consolidation protocols leading to more (vs. less) solid memory traces would trigger substantial brain responses and lead to more accurate memory performance. With respect to modified episodes, we expected the involvement of (para)hippocampal regions in the formation of false memories.

**Study 3** aimed to identify distinct neural signatures underlying the experience of repetitive and varying PEs. Both repetitive and varying PEs were expected leading to increased brain activity in regions typical for experiencing PEs, but each further engaging differential areas. Specifically, varying compared to repetitive alternative versions were hypothesized to trigger stronger activation in the hippocampal formation leading to memory traces competing stronger with recall of original objects.

# 3 Research Articles

## 3.1 Study 1: Seeing What I Did (Not): Cerebral and Behavioral Effects of Agency and Perspective on Episodic Memory Re-activation

Running title: Agency and Perspective in Episodic Memory

Benjamin Jainta, Sophie Siestrup, Nadiya El-Sourani, Ima Trempler, Moritz F. Wurm,
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# Seeing What I Did (Not): Cerebral and Behavioral Effects of Agency and Perspective on Episodic Memory Re-activation

**Benjamin Jainta[1]*, Sophie Siestrup[1,2], Nadiya El-Sourani[1], Ima Trempler[1,2], Moritz F. Wurm[3], Markus Werning[4], Sen Cheng[5] and Ricarda I. Schubotz[1,2]**

[1] Department of Psychology, University of Münster, Münster, Germany, [2] Otto Creutzfeldt Center for Cognitive and Behavioral Neuroscience, University of Münster, Münster, Germany, [3] Center for Mind/Brain Sciences, University of Trento, Rovereto, Italy, [4] Department of Philosophy, Ruhr University Bochum, Bochum, Germany, [5] Institute for Neural Computation, Ruhr University Bochum, Bochum, Germany

Intuitively, we assume that we remember episodes better when we actively participated in them and were not mere observers. Independently of this, we can recall episodes from either the first-person perspective (1pp) or the third-person perspective (3pp). In this functional magnetic resonance imaging (fMRI) study, we tested whether agency and perspective modulate neural activity during memory retrieval and subsequently enhance memory performance. Subjects encoded a set of different episodes by either imitating or only observing videos that showed short toy stories. A week later, we conducted fMRI and cued episodic retrieval by presenting the original videos, or slightly modified versions thereof, from 1pp or from 3pp. The hippocampal formation was sensitive to self-performed vs. only observed actions only when there was an episodic mismatch. In a post-fMRI memory test a history of self-performance did not improve behavioral memory performance. However, modified videos were often (falsely) accepted as showing truly experienced episodes when: (i) they were already presented in this modified version during fMRI or (ii) they were presented in their original form during fMRI but from 3pp. While the overall effect of modification was strong, the effects of perspective and agency were more subtle. Together, our findings demonstrate that self-performance and self-perspective modulate the strength of a memory trace in different ways. Even when memory performance remains the same for different agentive states, the brain is capable of detecting mismatching information. Re-experiencing the latter impairs memory performance as well as retrieving encoded episodes from 3pp.

**Keywords: fMRI, episodic memory, perspective, agency, expectation violation, action observation, action imitation**

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*Szu-Han Wang,*
*University of Edinburgh,*
*United Kingdom*
*Nicholas L. Balderston,*
*University of Pennsylvania,*
*United States*

****Correspondence:***
*Benjamin Jainta*
*bjainta@uni-muenster.de*

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*Jainta B, Siestrup S, El-Sourani N,*
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## INTRODUCTION

Episodic memories enable us to retrieve information about events from our personal past, including when and where they were experienced (Tulving, 2002). Disturbingly, we have learned that episodic memories are prone to change and decay (Roediger and Butler, 2011; Nader, 2015; Lee et al., 2017). This slow and progressive modification process is presumably fueled by retrieval

(Roediger and Butler, 2011; Nader, 2015; Lee et al., 2017), meaning that each time we retrieve an episode, it may undergo subtle revision.

At first glance, episodic memory modification appears to result from some imperfection of the conservative mechanisms our nervous system is equipped with. However, modification of episodic memory may indeed be functional. A fundamental role of episodic memory is the imagination and prediction of the potential future, coined *mental time travel* (Tulving, 2002). It is suggested that internal models derived from our long-term memories inform future choices and behaviors based on previous experiences. Nevertheless, in an ever-changing world, a prerequisite to maintain the efficiency and validity of such internal models is to open them for the integration of new experiences. This updating process is initiated by prediction errors (Exton-McGuinness et al., 2015; Fernández et al., 2016). Accordingly, episodic memories are not only exploited in the course of envisaging the future but are gradually updated by matching them to the current experiences when retrieved.

A major question that derives from this is which conditions render the memory of a truly experienced episode more or less susceptible to later modification. According to recent studies, some subtle breaches of expectation during re-experiencing the original episode is deemed a trigger for such modifications (Sinclair and Barense, 2019). In the current fMRI study, we took advantage of this effect of prediction errors to investigate the influence of two factors on the susceptibility of episodic memory. We employed videos of original episodes that participants had experienced in the lab, and introduced subtle breaches of expectation by modifying either a detail of content (substituting an object) or a detail of structure (swapping two adjacent action steps) in a subset of these videos. We presented both original and modified videos repeatedly during the fMRI session. This was followed by a memory test that assessed memory performance as an indicator of potential episodic updating. Here, we manipulated two factors that we hypothesized would influence an episode's susceptibility to change:

First, we reasoned that episodes in which we were agents are less prone to modification than those in which we were only observers (factor AGENCY). It was found that self-performed episodes are remembered better than only observed ones (Hornstein and Mulligan, 2001). Moreover, event-related brain potentials differentiate between the re-activation of performed and only observed actions (Senkfor et al., 2002; Leynes and Kakadia, 2013).

Second, we considered that cueing the re-activation of an episode from the first-person or "field" perspective provides a more powerful and vivid re-experience of the original episode than cueing from the third-person or "observer" perspective (factor PERSPECTIVE). It has been reported that episodes remembered (primarily) from the first-person perspective are recalled more accurately and vividly when compared to those (primarily) retrieved from a third-person perspective (Rice and Rubin, 2009; Marcotti and St Jacques, 2018). Also, adopting a first-person perspective as compared to a third-person perspective during retrieval was found to increase activity in the amygdala, signaling greater subjective emotionality (Eich et al., 2009). Yet, another fMRI study reported significant brain activity for third versus first-person perspective retrieval, but no significant clusters for the opposite contrast (Grol et al., 2017).

Thus, self-performance and self-perspective were expected to hamper modification of the original episode, manifesting in high correct rejection scores in the MRI memory test, and a stable surprise-related BOLD response to the manipulated episode videos. In order to test these hypotheses, participants were filmed during encoding of episodic events while either imitating or merely observing PLAYMOBIL®-based action stories which were presented in original or modified versions during fMRI in two different perspectives. As we typically experience the world from 1pp, participants are expected to experience this perspective as more persuasive with regard to the representation of themselves in the videos. Thus, by reactivating these episodes and violating participants' expectations during fMRI we aimed at triggering internal model updating and manipulating memory performance.

In line with prior research (Schiffer et al., 2012, 2013; Siestrup et al., 2021), modified episode videos were expected to trigger substantial brain responses. Therefore, we expected these responses to be stronger for formerly self-performed than for merely observed episodes (H1a), and for videos presenting episodes from the first-person as compared to the third-person perspective (H1b). As to the specific network we expected for the violation response, our hypotheses were mainly focused on the hippocampal formation according to its key role in the re-activation of episodic memories (Rugg and Vilberg, 2013; Jeong et al., 2015). The hippocampal formation is taken to contribute to associative learning, the detection of associative mismatches and the generation of associative predictions (Kumaran and Maguire, 2006; Chen et al., 2011). Moreover, we may see activity in the medial frontal cortex (MFC) which was found to be involved in the processing of competing information for existing episodes, i.e., updating an internal model through new information in order to ensure predictive success (Schiffer et al., 2012, 2013).

With regard to specific behavioral hypotheses, we expected that episodic memories were updated due to repeated presentations of manipulated videos, and accordingly, they should be misclassified as originally experienced during episodic encoding (H2). This hypothesis has been addressed in detail in Siestrup et al. (2021). Moreover, false acceptance of modified videos should be higher for videos that show previously only observed episodes (H3a) and for videos that showed episodes from the third-person perspective (H3b). To rule out the possibility that effects were due to a generalized acceptance bias, we additionally presented entirely new episode videos ("novels") that we expected participants to classify as new (H4). Regarding reaction time (RT), we did not have any *a priori* hypotheses. Nevertheless, RT has been used previously as an indicator for the length of task-related cognitive processing (Barber et al., 2016). Further, longer RTs were suggested to represent the costs of higher demands in cognitive processing during retrieval (Noppeney and Price, 2004). Therefore, we decided to investigate RTs exploratorily.

## MATERIALS AND METHODS

### Participants

Forty female right-handed volunteers were recruited to participate in two training sessions and one fMRI scan. Two participants completed the training but did not return for the fMRI session. Additionally, two participants had to be excluded from the analyses of fMRI data due to technical difficulties during the acquisition of functional data or dizziness and nausea during the fMRI session. Of the 36 participants included in the statistical analysis (*M* = 22.67, *SD* = 2.40 years old; range 18–28 years), none reported a history of neurological or psychiatric disorders, or substances abuse. One additional participant had to be excluded for the analysis of the post-fMRI memory test due to misunderstood instructions. As the presented videos showed an actress, only females participated to ensure high self-identification with the stimulus material. The Edinburgh Handedness Inventory was used to assess (Oldfield, 1971) handedness. Participants were all right-handed and scores varied from +60 to +100 (*M* = 92.17, *SD* = 10.95). All participants had normal or corrected-to-normal vision. The study protocol was conducted in accordance with ethical standards of the Declaration of Helsinki and approved by the Local Ethics Committee of the University of Münster. Each participant signed an informed consent and received either reimbursement or course credits for their participation.

### Stimuli

Stimuli were comprised of 76 video clips (mean duration = 12.68 s, range 8.80–17.88 s) showing abstract, but complex stories played with PLAYMOBIL® toys to ensure encoding of unique episodes during training sessions. In each video, an actress was performing while wearing a black pullover and black rubber gloves. The back of the right glove was marked with a yellow dot to ease future imitation (Franz et al., 2007) from demo videos during training. Videos showed only the hands and forearms of the actress and toys, such as animals, characters, furniture, vehicles and tools. Each exact object was only used in one of the stories, which consisted of six to nine action steps (*M* = 7.36) and four to 14 separable objects (*M* = 7).

The toy-based stories were filmed on a matte white paper background using a digital reflex camera (Nikon D5300) which was centered above the table and faced straight down. Congruent with the area captured by the camera, a frame (47.5 × 28 cm) was taped on the paper background to visually enclose the camera section for the actress. Every single object needed to replay the story was placed next to the camera section. For a schematic overview of the filming setup, see **Figure 1**. Videos had a resolution of 1920 × 1080 px and 25 frames per second. All videos were edited with Adobe Premiere Pro CC (Adobe Systems Software, Dublin, Ireland, Version 12.1.2) so that each video started and ended with seven frames showing only background. Original filming perspective was the third-person (or observer) perspective (3pp). In order to create the first-person (or field) perspective (1pp), videos were rotated by 180° as done in a previous study (Wurm and Schubotz, 2018), allowing us to establish the factor PERSPECTIVE during the fMRI session.

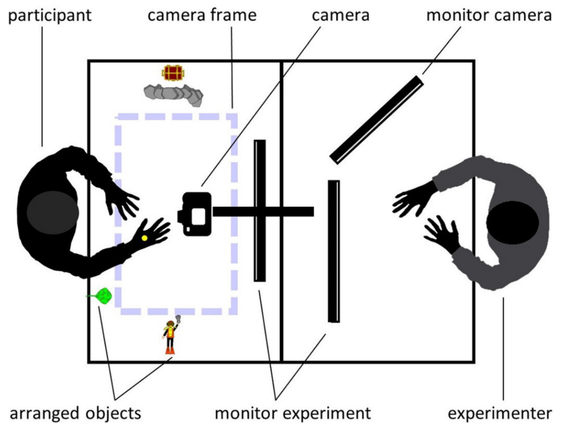

**FIGURE 1 |** Schematic overview of the filming setup during training sessions. Objects for each story were placed around the camera section (dashed lines). Trials were presented simultaneously for both, experimenter and participant. The participant's imitation attempts were filmed using the above-mounted camera. The experimenter watched the participant's performance during imitation trials on an additional screen.

A total set of 30 stories was examined in two preceding pilot studies (A and B) to investigate the difficulty of (1) imitating (based on the number of attempts needed to correctly imitate the story three times), (2) interpreting (based on the number of attempts and errors in description), and (3) identifying the story as part of training. Based on this screening, six stories were excluded.

Of the remaining 24 stories, there were three different versions of each, one original and two modified ones. The original versions were presented to participants, imitated or observed and described only. The modified versions involved either a structure-based modification (*str*), in which two adjacent action steps were swapped to elicit a sequential surprise, or a content-based modification (*con*), in which an object was swapped to elicit an object-semantic surprise (see **Figure 2** for an illustration). Effects regarding the factor modification (str, con) are only addressed in a companion paper (Siestrup et al., 2021). Note that the factors addressed in this paper were statistically independent of those reported in the mentioned paper. Modifications in the videos never occurred in the first two or last two actions steps of a story. Furthermore, four stories were additionally presented in only one version each during the fMRI session, which served as a control condition (hereafter referred to as "novels").

### Training Procedure

The training consisted of two sessions (approximately 2.0 and 1.5 h) on two consecutive days. In order to avoid fatigue or motivational decrease due to the long duration of the task, we chose to split the training over two consecutive days. During training, participants imitated half of the 24 stories

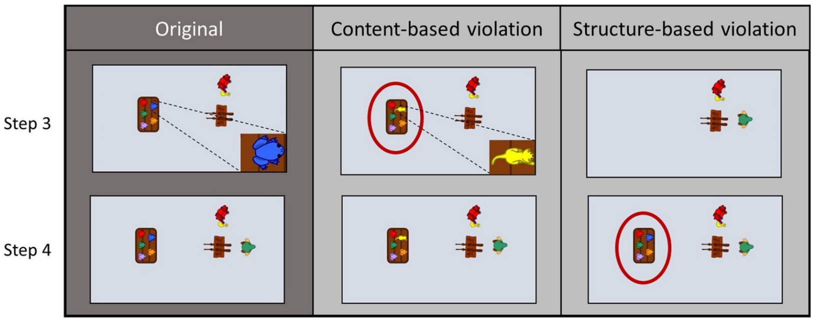

**FIGURE 2 |** Three different versions of two adjacent action steps for the story "shooting gallery". Sample video frames of the original version **(left column)** show how a table with five different colored frogs is placed (step 3) before the fair visitor with the green hat enters the scene (step 4). In the content-based modification **(middle column)** the blue frog on the table is replaced by a yellow cat, while in the structure-based modification **(right column)** the table with the five different colored frogs is placed (step 4) only after the fair visitor entered the scene (step 3).

from the original video clips and solely observed the other half. Each training session consisted of an imitation block and an observation block. Additionally, the first session included a short practice to get used to observing, imitating, and describing the action videos.

Twenty four stories were organized in four blocks (A1, B1, A2, B2; see **Figure 3**), each consisting of six videos and balanced for the number of actions steps. The assignment of videos to blocks remained the same while the running order of the videos was randomized in each block. Participants either imitated videos of blocks A1 and A2 and only observed videos of blocks B1 and B2 or vice versa, implementing the factor *AGENCY (imi, obs)*. The blocks and block order were balanced among participants. Thus, all actions were equally often imitated or only observed in the course of the study. Further, half of the participants started with an imitation block while the other half started with an observation block after the practice phase, and vice versa on the second training day.

To determine the number of video presentations needed to correctly imitate an action, we conducted two pilot studies. When participants were free to choose the number of video presentations (pilot study A), they watched a demo video a median of four times. In addition, we controlled whether the chosen number was suitable to imitate the actions from our set of stories (pilot study B). Based on our pilot data, subjects were presented with each demo video five times during the imitation blocks of the training session (four times from 3pp, once from 1pp). To ensure accurate encoding of the stories, participants had to correctly imitate each action three times. To counterbalance the different perspective experiences during the imitation and observation blocks, demo videos were presented in the observation blocks from both perspectives (four times from 3pp and four times from 1pp). With respect to the recognizability of the actions, the toys for each action in each block were arranged around the camera section (**Figure 1**) in the same way as when original versions were created.

During the imitation blocks, participants were asked to imitate actions as accurately as possible with regard to object orientation, speed, hand position etc. To ensure accurate encoding of the episodes, only trials without errors were classified as "successful attempt." If participants made a mistake, the experimenter interrupted them immediately and subjects had to rearrange the objects around the camera section and start again. The number of imitation attempts was not limited.

After subjects had imitated or merely observed an action, they were asked to give a detailed description of the story. A successful description included all the action steps in the correct order, including all objects that appeared in the correct color and the actions performed by the characters in the story. In this way, we ensured that the participants were attentive and understood the story correctly. If a participant made a mistake during the description, the experimenter interrupted them immediately and pointed out the error. The participants where then asked to start describing the current story again. The number of attempts to describe a story was not limited.

## Cover Story

Participants were told that they would be filmed during action execution and some of these videos would be presented during the fMRI experiment. This cover story was used to ensure that, maintaining a high level of standardization of the stimuli, there was still a personal identification with the actress in the videos.

To test the cover story, we tested participants' identification with the actor in the videos in another pilot study (B) one week after the training. To do so, we asked 16 independent participants to rate on a scale from 1 ("no") to 4 ("yes") whether they believed they appeared in the presented video ("Was this you in the video?"). A repeated measures ANOVA (rmANOVA) revealed a significant main effect of AGENCY [$F_{(1,15)} = 33.130$, $p < 0.001$]: Stronger identification was found for videos that participants had previously imitated ($M = 2.89 \pm 0.11$) (mean ± standard error of mean) than for those that had previously observed only ($M = 2.12 \pm 0.15$). Additionally, participants indicated that 45% of the videos showed themselves ($M = 45\% \pm 2.28\%$, Range = 20–80%). As a reminder, although they were filmed during training, none of the videos showed the participants; it was always the same

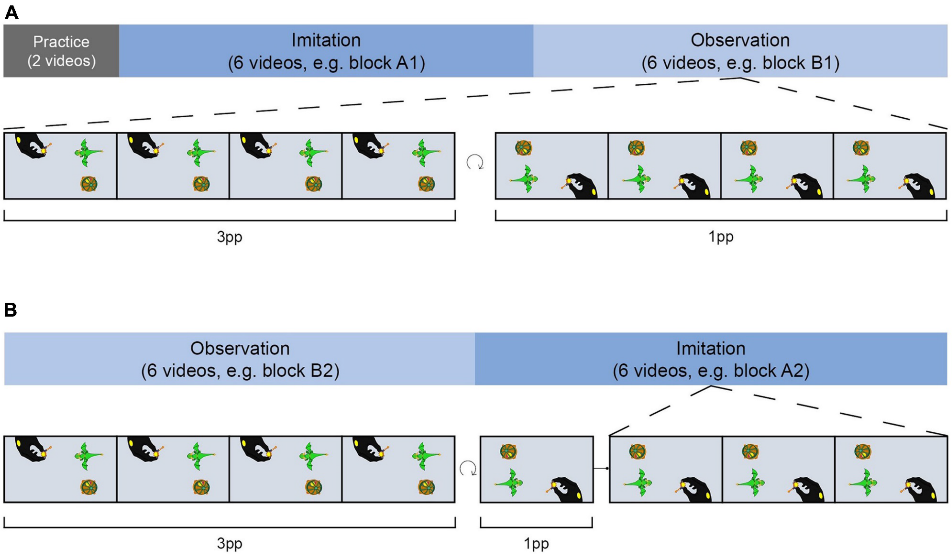

**FIGURE 3 |** Training procedure. Training took place on two consecutive days. Half of the actions were imitated and the other half were only observed by participants. Imitation and observation videos were presented within blocks of six videos each. **(A)** After a short practice on the first day, participants either started the training with an imitation block on the first **(A)** and an observation block on the second day **(B)** or vice versa. In the imitation block, each demo video was presented four times from 3pp and one time from 1pp before participants had to accurately imitate each action three times. During observation blocks, participants were presented with demo videos four times from 3pp and four times from 1pp. At the end of each trial, participants had to provide a detailed description of the action story.

actress. These results suggest that participants believed the cover story and were largely convinced that they were seeing videos of themselves during testing.

## Functional Magnetic Resonance Imaging Session

The fMRI experiment lasted approximately 50 min. Participants had already practiced the task briefly at the end of the second training session, and the practice trials were not used again in the fMRI session. Participants were presented with original and modified videos of the previously encoded stories. Each participant saw only either the original (*ori*) or the modified (*str*/*con*) version of a story. Out of the 24 stories encoded during training session, eight videos were presented in the original, eight in a structure modified and eight in a content modified version. Stories were assigned to each condition in a counterbalanced manner between participants, i.e., each video was presented equally often in each condition. With regard to the training procedure, half of the presented videos during fMRI showed stories that were previously imitated (imi) while the other half showed only observed videos (obs). The videos were presented either from the 1pp or from the 3pp, establishing the factor PERSPECTIVE. The assignment of videos to retrieval cueing perspective was counterbalanced among participants. We thereby obtained a 3 × 2 × 2 within-subject design with twelve experimental conditions, i.e., MODIFICATION (ori, str, con) × AGENCY (imi, obs) × PERSPECTIVE (1pp, 3pp). Please note that we aggregated content- and structure-based conditions which together included double as many trials as original versions and will be referred to as modified versions (mod) in the following sections. In each of the resulting 12 factorial combinations, two stories were presented six times each. The two stories contained actions of which one had been encoded during the first and the other one during the second training session. Four novel actions were included in the fMRI session to serve as a control condition, of which two were presented from 1pp and two from 3pp.

After 38.89% of the videos, a short description was presented (see **Figure 4**) that either matched or did not match the content of the preceding video (question trials). These question trials were used to ensure that participants attentively watched and recognized the action videos as shown in a previous study (El-Sourani et al., 2018). Accordingly, participants had to either accept or reject the description using two predetermined buttons on a response box. Questions were presented for a maximum of 3 s or until participants responded. Participants received written feedback (correct/incorrect/too late) after each question. During the experiment, each video was shown once with a matching description and once with a non-matching description.

The fMRI experiment comprised 242 trials divided into 6 blocks with 40 to 41 trials each. Each of these blocks contained 24 videos of previously encoded actions, three null events in which only a fixation cross was presented for 7–10 s, and 9–10 questions, of which approximately half were to be accepted and the other half rejected. In addition, each of the four novel videos was presented once per block. Thus, the entire experiment contained 144 video trials of previously encountered episodes,

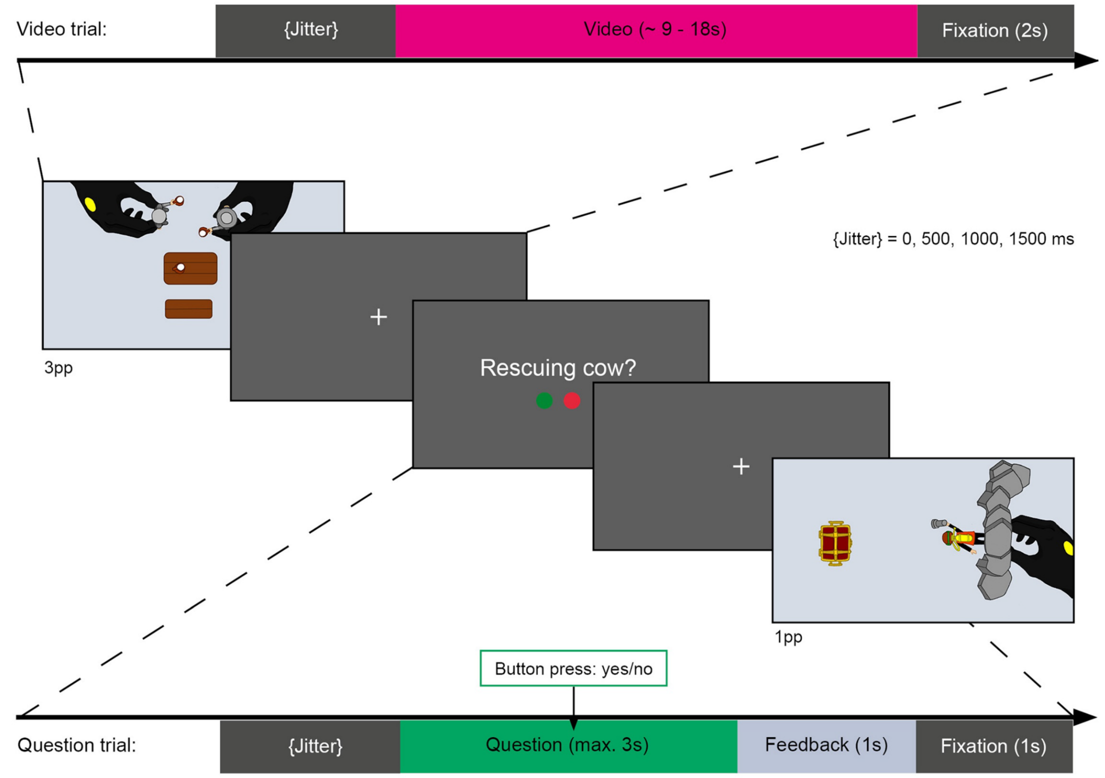

**FIGURE 4 |** Schematic illustration of task during fMRI session. Top bar showing duration and sequence of a video trial. Video trials contained a variable jitter (0, 500, 1000, or 1500 ms of fixation), a video showing a PLAYMOBIL® story (approx. 9 – 18 s) and a second fixation cross (2 s) serving as an interstimulus interval (ISI). Video trials were presented from an allocentric perspective (3pp, first image) or an egocentric perspective (1pp, last image). After some of the videos, a question regarding the action shown in the preceding video was presented. Question trials consisted of a variable jitter, a question presentation (max. 3 s or terminated by response) and an ISI, containing a 1 s feedback presentation ("correct," "incorrect," or "too slow") and a 1 s fixation cross. Participants had to respond by accepting (right index finger) or rejecting (right middle finger) the presented action description via a response box.

18 null events, 56 question trials, and 24 novel video trials. Trials were variably jittered (0, 500, 1000 or 1500 ms) and ended with a fixation cross (2 s after videos or 1 s after questions). The trial order was pseudorandomized to balance the transition probabilities between conditions and the order of presentation of the conditions within each block. A maximum of four video trials were presented consecutively throughout the experiment.

### Functional Magnetic Resonance Imaging Acquisition

Imaging was performed on a 3-Tesla Siemens Magnetom Prisma MR tomograph using a 20-channel head coil and took place approximately one week after the second session ($M$ = 7.42 days, $SD$ = 0.9 days). Participants were located in a supine position on the scanner bed with their right index and middle finger positioned on two predetermined response buttons on a response box. To minimize arm and head motions, arms and heads were tightly fixated with form-fitting cushions. Additionally, participants were provided with earplugs and headphones to attenuate scanner noise. Stimulus presentation and response coding were performed using Presentation 20.3 (Neurobehavioral Systems, San Francisco, CA, United States). Stimuli were projected onto a screen at the end of the scanner bore. Participants saw the screen on an individually adjusted mirror mounted to the head coil.

Prior to functional imaging, high resolution T1 weighted anatomical images were obtained with a 3D-multiplanar rapidly acquired gradient-echo (MPRAGE) sequence. 192 slices with a thickness of 1 mm were acquired, using a repetition time (TR) of 2130 ms, an echo time (TE) of 2.28 ms, a flip angle of 8° and a field of view (FoV) of 256 × 256 $mm^2$. Functional images of the whole brain were acquired in interleaved order along the bicomissural plane (AC–PC) using a gradient-echo echoplanar imaging (EPI) sequence sensitive to BOLD contrast. Thirty-three axial slices with a thickness of 3 mm were obtained in an interleaved order, using a TR of 2000 ms, a TE of 30 ms, a FoV of 192 × 192 $mm^2$ and a flip angle of 90°.

Imaging data were processed using SPM12 (Wellcome, Trust, London, United Kingdom) implemented in MATLAB R2018b. First, slice time correction to the middle slice was performed, followed by movement correction and realignment to the mean image. Then, individual structural scan was co-registered to the mean functional image and segmented into native tissue components. Functional and structural images were normalized into the standard MNI space (Montreal neurological Institute, Montreal, QC, Canada). Spatial smoothing was based on a Gaussian kernel of full-width at half maximum (FWHM) of 8 mm. Additionally, a 128 s high-pass temporal filter was applied.

### Functional Magnetic Resonance Imaging Design Specifications

The statistical analysis of the fMRI data was based on a least-squares estimation using the general linear model (GLM) for serially autocorrelated observations (Friston et al., 1994; Worsley and Friston, 1995). The GLM convolved regressors with a canonical hemodynamic response function and contained a total of 18 regressors: eight predictors for the experimental conditions, one predictor for null events, one for question trials, two for novel videos, and six regressors of nuisance for the motion parameters (three translations, three rotations). Video trials were assigned to the eight experimental condition regressors with regard to whether they (1) showed an original (*ori*) or a modified version (*mod*) of previously (2) imitated (*imi*) or only observed (*obs*) action stories (3) presented in a 1pp or a 3pp. Activations were analyzed time-locked to the onset of the videos and the analyzed epoch comprised the full duration of the presented videos (8.80–17.88 s). The modeled activation of null events (7–10 s) and questions (max. 3 s) was time-locked to their respective onsets. Question trials were modeled as events. Novel videos (nov) were assigned to two regressors regarding their stimulus-presentation mode (1pp vs. 3pp).

On the first level of the analysis, we applied gray matter masking. Here, we used smoothed individual normalized gray matter images (8 mm FWHM) thresholded at 0.2 using ImCalc in SPM12 creating a binary mask. On the second level, we performed group analyses by using one-sample $t$-tests across participants. A false discovery rate (FDR) correction with a threshold of $p < 0.05$ or higher (peak level) was applied. When no significant activation clusters were found using this threshold, we applied a threshold of $p < 0.001$, uncorrected for multiple comparisons. This is a common approach when specific neuroanatomic hypotheses are investigated (Farrer and Frith, 2002; Mechelli et al., 2006; Kumaran and Maguire, 2007).

To investigate whether brain activity differs for retrieved action episodes compared to novel stories, we calculated first-level $t$ contrasts for ori > nov and mod > nov. Because original episodes as well as the slightly modified episodes should lead to the retrieval of episodic memories in contrast to previously unencoded episodes (novels), we built the conjunction of these contrasts. This approach was used to provide (i) the validation for successful retrieval of encoded episodes and (ii) the basis that effects of AGENCY and/or PERSPECTIVE underlie episodic memory retrieval.

To test the effects of perspective, we built separate contrasts of 1pp > 3pp and 3pp > 1pp for original and modified episodes. Then, we analyzed whether perspective had a specific effect on episodic retrieval as compared to novel videos. To this end, we also calculated the 1pp vs. 3pp contrast for novel videos and considered the interaction. Confounding effects of modification on perspective were ruled out by building conjunctions over perspective contrasts of original and modified episodes. To test the effects of agency, we obtained a conjunction for imitated vs. only observed original and modified episodes to analyze the impact of agency ($\text{ori}_{\text{imi}} > \text{ori}_{\text{obs}} \cap \text{mod}_{\text{imi}} > \text{mod}_{\text{obs}}$).

To explore hippocampal activity for original vs. modified episodes that have either been imitated or only observed during training, we conducted ROI analyses for left and right hippocampus by extracting beta values for the regressors $\text{ori}_{\text{imi}}$, $\text{ori}_{\text{obs}}$, $\text{mod}_{\text{imi}}$, and $\text{mod}_{\text{obs}}$. Mean beta values for each regressor were extracted using the MarsBaR Toolbox (Brett et al., 2002). For statistical analysis, we used a three-way rmANOVA with the factors HEMISPHERE (left, right), MODIFICATION (ori, mod) and AGENCY (imi, obs) and post-hoc pairwise $t$-tests for $\text{ori}_{\text{imi}}$ vs. $\text{ori}_{\text{obs}}$ and $\text{mod}_{\text{imi}}$ vs. $\text{mod}_{\text{obs}}$. Here, we were specifically interested in the effects of agency on hippocampal activity. Therefore, we additionally performed two paired $t$-tests (one-tailed) for the comparisons of $\text{ori}_{\text{imi}} > \text{ori}_{\text{obs}}$ and $\text{mod}_{\text{imi}} > \text{mod}_{\text{obs}}$ in each hemisphere separately. We applied a significance level of $\alpha = 0.05$, Bonferroni–Holm-adjusted for multiple comparisons (Holm, 1979). To this end, anatomical ROIs of the left and right hippocampus (including the CA1, CA2, CA3, dentate gyrus, subiculum, entorhinal cortex and the hippocampal-amygdaloid transition region) were created from probabilistic maps from the Julich-Brain Cytoarchitectonic Atlas (Amunts et al., 2020). A threshold of 0.2 was implemented in ImCalc and final ROIs were created using the MarsBaR toolbox (Brett et al., 2002) in SPM12. Further, we used Pearson's correlation coefficient to examine the relationships between mean beta values and behavioral memory performance for original and modified videos separated by MODIFICATION during fMRI and AGENCY.

## Memory Test

After the fMRI experiment, participants conducted a memory test which took approximately 15 min. In a separate room, subjects were instructed to watch action videos on a laptop and to rate whether they remember the exact story presented from the training session. Responses were measured on a four-point Likert scale (1: *yes*; 2: *rather yes*; 3: *rather no*; 4: *no*) by pressing one of four marked keys on the laptop's keyboard. There was no time restriction for responses, but extreme outliers were removed as described in the following section.

Participants were presented with two versions of each of the stories they had seen during fMRI, an original and a modified version. If they had seen a modified version during fMRI, they were now presented with the same modified version as well as the corresponding original version. If participants had seen the original version during the fMRI, they now saw a corresponding modified version in addition to the original. Thus, responses were always given for an original and a modified video of the exact same story that had been seen for the first-time during training. Each novel video was presented twice. Thus, participants had to respond to a total of 56 videos. These responses indicated how well the participants could remember the individual storylines.

## Behavioral Data Analysis

Behavioral data from the fMRI session and the post fMRI memory test were analyzed using RStudio (R Core Team, 2019; version 1.2.5001).

Performance during the fMRI session was assessed by correct response rates and RTs on correctly answered question trials.

For the analysis of the memory test, we used participants' mean rating times, i.e., RTs of correct and incorrect responses, and mean ratings on remembering a presented episode from the training on a four-point Likert scale. Please note that high ratings mean low acceptance, while low ratings mean high acceptance. After completing the memory test, one participant reported difficulties in understanding the task correctly. Thus, we excluded data from this subject from the behavioral analysis of the memory test. Considering rating times during the memory test, a single trial was excluded in advance as one participant left the laptop to talk to the experimenter.

Data distribution was tested by using the Shapiro–Wilk Test. When RTs and rating times did not fit normal distribution, we applied logarithmic transformation to make data conform to normality in order to use parametric rmANOVA. As ratings were not normally distributed, we used a non-parametric rmANOVA based on aligned rank data (Wobbrock et al., 2011). For parametric and non-parametric rmANOVAs, we used a 2 × 2 × 2 within-subject design with the factors MODIFICATION (ori, mod) during fMRI, encoding AGENCY (imi, obs) and PERSPECTIVE (1pp, 3pp). Please note, that we aggregated modified videos (str, con) for the analysis of behavioral responses as the main focus of this study was to investigate the effects of agency and perspective on true and false episodic memories. For a more detailed analysis of the modification conditions (con, str), see Siestrup et al. (2021). We separately investigated mean ratings and rating times for original and modified videos during memory test in order to generate higher discriminatory power for subtle effects on true and false memories. *Post hoc* pair-wise comparisons were conducted with paired $t$-tests (one-tailed). With regard to our control condition of novel stories, we used paired sample $t$-tests (two-tailed).

The significance level for all behavioral analyses was set to $p < 0.05$. In order to compensate for multiple comparisons, $p$-values were adjusted using the Bonferroni–Holm correction (Holm, 1979).

# RESULTS

## Behavioral Results of the Functional Magnetic Resonance Imaging Session

During the fMRI experiment, participants rejected short descriptions of each preceding video as inaccurate or accepted them as accurate by selecting the corresponding response button. As subjects very rarely responded incorrect to questions during fMRI, we did not find any significant effect in correct response rates. Thus, we only report descriptive values. Participants correctly answered 98.2% ± 0.55% (mean ± standard error of mean) of question trials following an original video and 98.3% ± 0.38% following a modified video. For our control condition, participants correctly answered 96.8% ± 1.04% of question trials following a new video. Bar charts of the three-factor design regarding the correct response rates are provided in **Supplementary Figure 1**.

With regard to RT on correct trials, a three-way rmANOVA with the factors story MODIFICATION (original, modified), stimulus presentation mode PERSPECTIVE (1pp, 3pp) and pre-fMRI training mode AGENCY (imitated, observed) revealed a significant main effect for the factor PERSPECTIVE [$F_{(1,35)} = 6.39$, $p = 0.02$]. Thus, subjects were significantly faster when presented with a video from 1pp ($M_{1pp} = 958.66$ ms ± 20.12 ms) than from 3pp ($M_{3pp} = 980.06$ ms ± 20.63 ms). There were no significant main effects for the factors MODIFICATION ($M_{ori} = 963.72$ ms ± 21.68 ms; $M_{mod} = 975$ ms ± 19.02 ms) or AGENCY ($M_{imi} = 977.05$ ms ± 20.92 ms; $M_{obs} = 961.68$ ms ± 19.85 ms).

In addition, we found a significant interaction effect of MODIFICATION and AGENCY [$F_{(1,35)} = 4.83$, $p = 0.03$]. Paired samples $t$-tests showed that participants were significantly slower when previously imitated episodes were presented in a modified ($M_{mod-imi} = 1001$ ms ± 38.16 ms) compared to an original version [$M_{ori-imi} = 953.86$ ms ± 41.15 ms; $t_{(35)} = 2.39$, $p = 0.01$] but also when compared to a modified version of an episode that had only been observed before [$M_{mod-obs} = 949.64$ ms ± 34.86 ms; $t_{(35)} = 4.14$, $p < 0.001$]. Accordingly, subjects took longer to recognize modified videos when these videos showed previously self-enacted stories. Further, we found a significant interaction of MODIFICATION and PERSPECTIVE [$F_{(1,35)} = 8.02$, $p = 0.007$]. When presented with a modified video from 1pp ($M_{mod-1pp} = 952.91$ ms ± 27.18 ms) participants were significantly slower [$t_{(35)} = 3.9$, $p < 0.001$] as compared to 3pp videos ($M_{mod-3pp} = 997.1$ ms ± 26.56 ms) while this was not the case for originals [$M_{ori-1pp} = 964.41$ ms ± 29.85 ms, $M_{ori-3pp} = 963.04$ ms ± 31.64 ms; $t_{(35)} = 0.28$]. There was also a significant interaction of AGENCY and PERSPECTIVE [$F_{(1,35)} = 4.88$, $p = 0.03$]. Participants were significantly slower when presented with a video showing a previously imitated episode from 1pp vs. 3pp [$M_{imi-1pp} = 952.83$ ms ± 29.64 ms, $M_{imi-3pp} = 1001.27$ ms ± 29.44 ms; $t_{(35)} = -2.96$, $p < 0.01$]. This was not the case for formerly only observed actions [$M_{obs-1pp} = 964.48$ ms ± 27.40 ms, $M_{obs-3pp} = 958.04$ ms ± 28.9 ms; $t_{(35)} = 0.61$, $p = 0.27$]. Finally, participants were significantly slower to respond to new videos from 1pp ($M_{nov-1pp} = 1064.06$ ms ± 52.07 ms) than from 3pp [$M_{nov-3pp} = 989.69$ ms ± 39.53 ms; $t_{(35)} = 2.34$, $p = 0.01$] (**Figure 5**).

## Functional Magnetic Resonance Imaging Results

### Main Effect of Episodic Reactivation

To investigate which brain regions are generally involved in episodic memory re-activation we contrasted formerly encoded with completely new stories. This was done separately for original

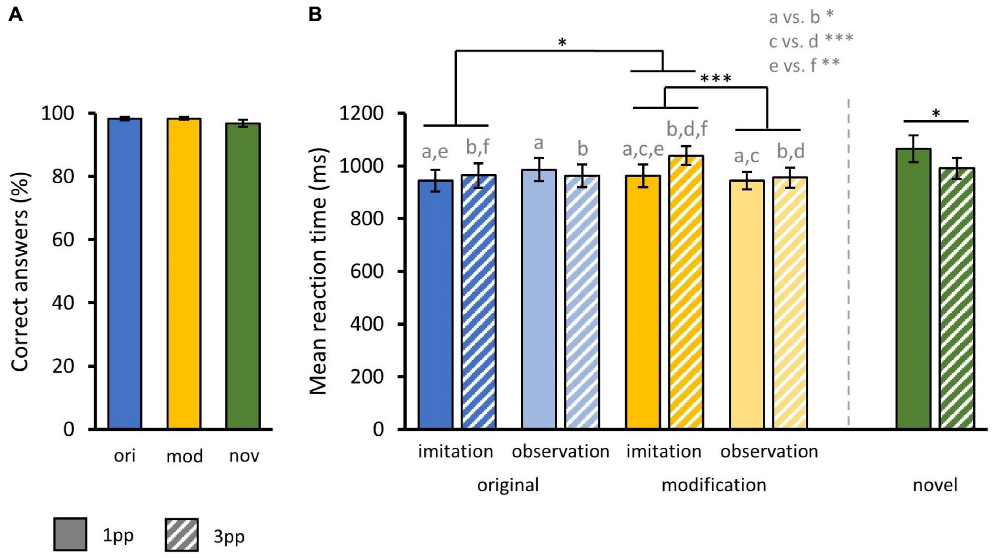

**FIGURE 5 |** Behavioral results from fMRI task. **(A)** Mean correct response rates for original (ori), modified (mod), and novel (nov) videos during fMRI action recognition task. **(B)** Mean reaction times for original and modified videos separated by the factors AGENCY (imitation, observation) and PERSPECTIVE (1pp, 3pp) and additionally for novels. Statistics: rmANOVA with *post hoc* paired *t*-tests; a vs. b = $p < 0.05$; c vs. d = $p < 0.001$; e vs. f = $p < 0.01$. **(A,B)** Bar charts show means and standard errors.

(ori > nov) and modified (mod > nov) episodes. We then built the conjunction of these two contrasts (ori > nov ∩ mod > nov) to determine regions that were active when participants retrieved episodic memories, no matter whether encountered in the original or a modified version. Here, we found significant activity in the left posterior mid cingulate cortex (pCC), the left posterior precuneus (pCUN), the right cuneus (CUN), the left anterior cingulate cortex (ACC), the bilateral midfrontal gyrus (MFG), the bilateral mid-Insula and the right lingual gyrus (LG) (**Table 1** and **Figure 6**). The reverse contrast (nov > ori) revealed a widespread activity pattern including increased activity in bilateral hippocampus (HC) (**Supplementary Figure 2** and **Supplementary Table 1**).

**TABLE 1 |** Peak activations from second-level whole-brain analyses of episodic effects.

| Area | *H* | Cluster extent (voxels) | MNI Coordinates | | | Z |
|---|---|---|---|---|---|---|
| | | | *x* | *y* | *z* | |
| ***(ori > nov) ∩ (mod > nov)*** | | | | | | |
| pCC | L | 120 | −3 | −25 | 35 | 5.40 |
| CUN | R | 209 | 18 | −91 | 23 | 5.38 |
| | L | | −6 | −100 | 17 | 4.46 |
| Posterior PCUN | L | 59 | −9 | −67 | 32 | 4.12 |
| ACC | L | | −3 | 26 | 20 | 3.65 |
| MFG | L | 10 | −39 | 44 | 20 | 3.94 |
| | R | 7 | 39 | 44 | 8 | 3.80 |
| Insula | L | 29 | 39 | 11 | −7 | 3.89 |
| | R | 18 | −36 | 8 | −7 | 4.13 |
| LG | R | 23 | 15 | −76 | −7 | 4.34 |

*H, hemisphere; L, left; R, right; MNI, Montreal Neurological Institute; PCUN, precuneus; pCC, posterior cingulate cortex; CUN, cuneus; ACC, anterior cingulate cortex; MFG, middle frontal gyrus; LG, lingual gyrus. FDR-corrected at p < 0.05.*

## Cerebral Effects of Former Self-Performance in Reactivated Episodes

To test the hypothesis that formerly self-performed episodes produce stronger neural activity than merely observed episodes, we first contrasted formerly imitated versus observed episodes for original ($\text{ori}_{\text{imi}} > \text{ori}_{\text{obs}}$) and modified videos ($\text{mod}_{\text{imi}} > \text{mod}_{\text{obs}}$). While we did not find any effect for the original videos, there was subthreshold activity for the modified episodes contrast (uncorr., $p < 0.001$) in the left hippocampus (HC; $x = -27$, $y = -22$, $z = -13$, $Z = 3.71$), the left posterior PCUN ($x = -6$, $y = -67$, $z = 23$, $Z = 3.83$) and the left MFC in Brodmann area 10 (BA 10; $x = -12$, $y = 56$, $z = 2$, $Z = 3.59$).

To further investigate the hypothesis that HC was more strongly involved in episodic memory for imitated vs. only observed episodes, we performed a region of interest (ROI) analysis. ROIs of the right and left HC were created using probabilistic maps from the Julich Brain Cytoarchitectonic Atlas (Amunts et al., 2020). We separately contrasted formerly self-performed and only observed actions for original ($\text{ori}_{\text{imi}}$, $\text{ori}_{\text{obs}}$) and modified episodes ($\text{mod}_{\text{imi}}$, $\text{mod}_{\text{obs}}$). We used a three-way rmANOVA with the factors HEMISPHERE, MODIFICATION and AGENCY and found a marginally significant interaction effect of MODIFICATION and AGENCY [$F_{(1,34)} = 3.57$, $p = 0.07$]. As the whole-brain contrast indicated stronger activation in the left HC, we exploratorily investigated the

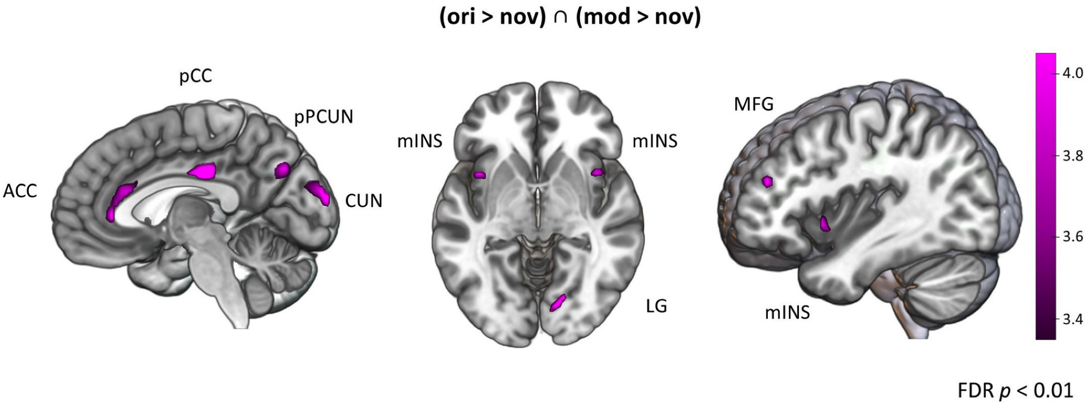

**FIGURE 6 |** Brain activation for episodes. Areas activated for action videos showing formerly experienced stories contrasted with novel stories [(*ori* > *nov*) ∩ (*mod* > *nov*)]. FDR-corrected *t*-map ($p < 0.05$). CUN, cuneus; PCUN, precuneus; pCC, posterior cingulate cortex; ACC, anterior cingulate cortex; MFG, middle frontal gyrus; mINS, mid-Insula; LG, lingual gyrus.

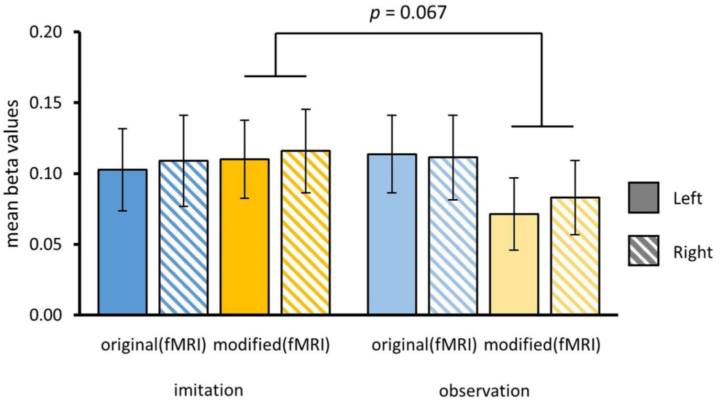

**FIGURE 7 |** Beta values for ROI of left and right hippocampal complex (HC). Beta values were separately extracted for original and modified videos for actions that have been formerly imitated or only observed. Contrasts were computed for each condition vs. implicit baseline. Bars show means and standard errors of means. Beta values were significantly higher in left hippocampus for imitated than only observed actions during presentation of modified videos.

interaction in both HC for original and modified versions. We did not find any significant main effect or further interactions. For the left HC, paired *t*-tests revealed that observed actions ($M_{mod-obs} = 0.07 \pm 0.03$) vs. self-performed ($M_{mod-imi} = 0.11 \pm 0.03$) produced decreased activity in left HC when presented in a modified version [$t_{(35)} = 2.19$, $p = 0.02$], whereas this was not the case for original versions [$M_{ori-imi} = 0.1 \pm 0.03$, $M_{ori-obs} = 0.11 \pm 0.03$; $t_{(35)} = -0.7$, $p = 0.24$]. Though descriptively showing a similar tendency, no significant effect was found for beta scores in the right HC ROI (**Figure 7**).

## Cerebral Effects of First-Person Perspective During Episode Reactivation

To test the hypothesis that episodic reactivation from the 1pp elicits a higher BOLD response than reactivation from the 3pp due to more vivid re-experiencing, we contrasted 1pp videos with 3pp videos separately for original and for modified stories. During presentation of an original episode from 1pp ($\mathrm{ori}_{1\mathrm{pp}} > \mathrm{ori}_{3\mathrm{pp}}$) we found more pronounced activity in the bilateral CUN. This effect was also found for modified videos ($\mathrm{mod}_{1\mathrm{pp}} > \mathrm{mod}_{3\mathrm{pp}}$). For completeness, we also report the effects of reversed contrasts, for which we had no hypotheses: Showing videos of original episodes from 3pp ($\mathrm{ori}_{3\mathrm{pp}} > \mathrm{ori}_{1\mathrm{pp}}$) resulted in increased activation in the right LG and the left dorsal PM (PMd), whereas presenting modified videos from 3pp ($\mathrm{mod}_{3\mathrm{pp}} > \mathrm{mod}_{1\mathrm{pp}}$) revealed activity in the bilateral inferior parietal lobe, the right LG, the right CUN, the right medial temporal gyrus and the left SMA (**Figure 8** and **Table 2**; FDR-corrected at $p < 0.05$).

In sharp contrast to these moderate effects, we found strong and widespread activity patterns for novel stories presented

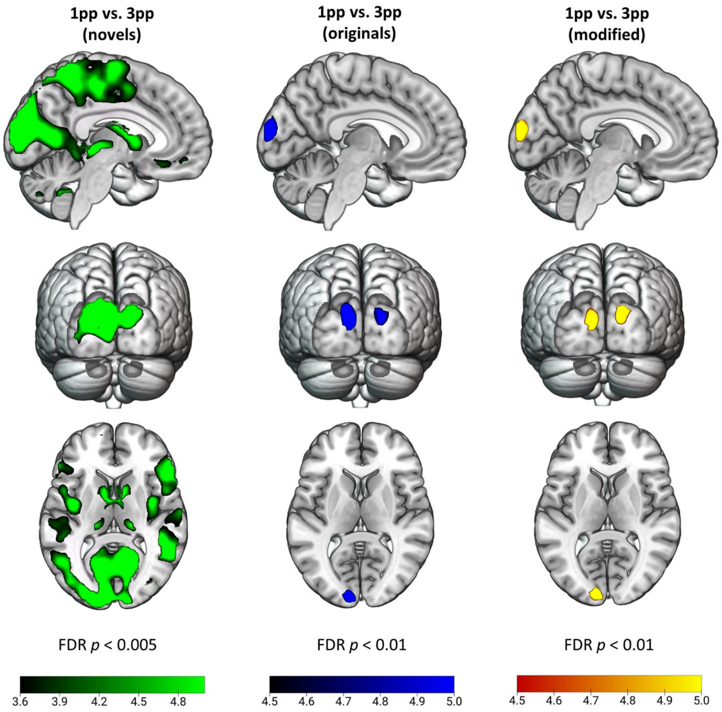

**FIGURE 8 |** Effects of perspective for novel (green), original (blue), and modified (yellow) stories. Activity patterns indicate enhanced activity for a first-person perspective (1pp) compared to a third-person perspective (3pp). For better visualization we show t-maps at $p < 0.005$ (FDR-corrected) for the novel videos, and $p < 0.01$ (FDR-corrected) for original and modified videos. New videos presented from 1pp led to increased activity in supplementary motor area, thalamus, posterior insula, cuneus, supramarginal gyrus and inferior frontal gyrus among others. Original and modified videos showed more engaged activation in bilateral cuneus.

from 1pp ($nov_{1pp} > nov_{3pp}$). Activation was higher in several areas as e.g., the left supramarginal gyrus (SMG) ($x = -54$, $y = -25$, $z = 44$, $Z = 7.67$), the right inferior PMd ($x = 54$, $y = 8$, $z = 29$, $Z = 5.27$), the left IFG ($x = 57$, $y = 32$, $z = 5$, $Z = 5.22$). Notably, the reverse comparison ($nov_{3pp} > nov_{1pp}$) did not yield any significant activation. To statistically validate the difference in perspective effects between encoded episodes and novel videos, we built the conjunction of the three contrasts $[(nov_{1pp} > nov_{3pp}) > (ori_{1pp} > ori_{3pp}) \cap (nov_{1pp} > nov_{3pp}) > (mod_{1pp} > mod_{3pp})]$. This revealed more pronounced activation for novels in a widespread set of areas, including the bilateral superior ventral premotor cortex (sPMv), anterior precuneus (aPCUN), the bilateral superior PM the right SMG, cuneus (CUN; extending from calcarine sulcus into cuneus), the bilateral superior temporal lobe (STL), the left lingual gyrus (LG) and the right fusiform gyrus (FG) (**Table 3** and **Figure 9**).

## Behavioral Results of the Post-functional Magnetic Resonance Imaging Memory Test

We analyzed memory performance by averaging responses to $original_{MT}$ and $modified_{MT}$ videos separately. We used two three-way rmANOVA based on aligned ranks with the factor stimulus $MODIFICATION_{fMRI}$ ($original_{fMRI}$, $modified_{fMRI}$), presentation mode PERSPECTIVE (1pp, 3pp) and pre-fMRI training mode AGENCY (imitated, observed).

First, we tested whether original episodes were rejected more often after repeated presentation in a modified version during fMRI. We found a significant main effect for the factor $MODIFICATION_{fMRI}$ [$F_{(1,34)} = 21.59$, $p < 0.001$] indicating that after repeatedly watching $modified_{fMRI}$ videos of a story ($M_{mod} = 1.27 \pm 0.04$), participants were less likely to accept originals videos as truly experienced compared to after re-experiencing $originals_{fMRI}$ during fMRI ($M_{ori} = 1.20 \pm 0.04$). There were no significant interaction effects nor did we find main effects of AGENCY or PERSPECTIVE.

Second, we examined whether modified episodes were more often misclassified as known from training in the memory test after repeated presentation in the scanner. Indeed, repeated presentation of $modified_{fMRI}$ videos ($M_{mod} = 2.14 \pm 0.07$) led to higher acceptance of modified versions than after previously experiencing the original stories ($M_{ori} = 2.48 \pm 0.08$), reflected in a significant main effect of $MODIFICATION_{fMRI}$ [$F_{(1,34)} = 14.94$, $p < 0.001$]. We found a significant interaction effect for the factors $MODIFICATION_{fMRI}$ and PERSPECTIVE [$F_{(1,34)} = 5.84$, $p = 0.02$] indicating that participants accepted

**TABLE 2 |** Peak activations from second-level whole-brain analyses of perspective effects in episodes.

| Area | H | Cluster extent (voxels) | MNI Coordinates | | | Z |
|---|---|---|---|---|---|---|
| | | | x | y | z | |
| ***$ori_{1pp} > ori_{3pp}$*** | | | | | | |
| CUN | L | 137 | –9 | –94 | 11 | 6.00 |
| | R | 61 | 18 | –91 | 14 | 4.07 |
| ***$ori_{3pp} > ori_{1pp}$*** | | | | | | |
| LG | R | 735 | 6 | –82 | –1 | INF |
| PMd | L | 13 | –51 | –13 | 53 | 4.07 |
| ***$mod_{1pp} > mod_{3pp}$*** | | | | | | |
| CUN | L | 109 | –9 | –94 | 14 | 5.52 |
| | R | 61 | 18 | –94 | 23 | 5.45 |
| ***$mod_{3pp} > mod_{1pp}$*** | | | | | | |
| IPL | L | 20 | –51 | –52 | 53 | 3.34 |
| | R | 25 | 54 | –55 | 47 | 3.44 |
| SMA | L | 28 | –9 | 26 | 47 | 3.60 |
| MTG | R | 28 | 42 | –64 | 11 | 3.60 |
| CalcS extending into CUN | R | 1064 | 6 | –85 | –1 | 7.59 |
| LG | R | | 15 | –73 | –7 | 7.11 |

*L, left; R, right; MNI, Montreal Neurological Institute; CUN, cuneus; LG, lingual gyrus; PMd, dorsal premotor cortex; IPL, inferior parietal lobe; SMA, supplementary motor area; MTG, medial temporal gyrus; CalcS, calcarine sulcus. FDR-corrected at p < 0.05.*

modified stories in the memory test more often when the presentation of original stories during fMRI occurred from 3pp ($M_{ori-3pp}$ = 2.39 ± 0.11) than from 1pp [$M_{ori-1pp}$ = 2.58 ± 0.12; $t_{(34)}$ = 1.86, $p$ = 0.04]. This was not the case for videos presented in a modified version during fMRI [$M_{mod-3pp}$ = 2.19 ± 0.1, $M_{mod-1pp}$ = 2.09 ± 0.1; $t_{(34)}$ = 0.65, $p$ = 0.74], suggesting that perspective had an effect on the retrieval of the original but not the modified videos during the subsequent memory test. Note that the perspective of presenting a story during the fMRI was maintained in the memory test. There was no interaction with AGENCY nor main effects of AGENCY or PERSPECTIVE (**Figures 10A,B**).

In addition, we calculated a three-way rmANOVA with the factors MODIFICATION$_{MT}$ (original$_{MT}$, modified$_{MT}$), PERSPECTIVE and AGENCY on rating times, including ratings for correct and false responses. Here we did not find any effect on mean rating times, but participants tended to respond faster to original versions ($M_{ori}$ = 687.97 ms ± 21.58 ms) compared to modified ones [$M_{mod}$ = 749.4 ms ± 34.16 ms; $F_{(1,34)}$ = 1.33, $p$ = 0.26] (**Figure 10C**).

Further, we calculated one-sided $t$-tests for responses and rating times for the new videos. Here, differences did not reach significance as participants showed overall low acceptance for novels. Descriptively, participants took longer to rate videos presented from 3pp [$M_{nov-1pp}$ = 642.05 ms ± 55.96 ms; $M_{nov-3pp}$ = 1002.25 ms ± 418.57 ms; $t_{(34)}$ = 0.66, $p$ = 0.26].

In order to examine the relationship between hippocampal activity and behavioral memory performance, correlations were computed between mean beta values in hippocampus with responses for original and modified videos during the post-fMRI memory test separated by the factors MODIFICATION (ori, mod) during fMRI and pre-fMRI AGENCY (imi, obs). As a result, there was no significant relationship between hippocampal activation and memory performance.

To summarize the behavioral results of the post-fMRI memory test, subjects took longer to rate whether they experienced a story during training when this story was presented with a slight modification. Correspondingly, videos that had already been presented in a modified version in the scanner were later more often mistaken for original episodes in this modified form. When

**TABLE 3 |** Peak activations from second-level whole-brain analyses of perspective effects.

| Area | H | Cluster extent (voxels) | MNI Coordinates | | | Z |
|---|---|---|---|---|---|---|
| | | | x | y | z | |
| ***(nov1pp > nov3pp) > (ori1pp > ori3pp) ∩ (nov1pp > nov3pp) > (mod1pp > mod3pp)*** | | | | | | |
| Postcentral gyrus | R | 12 | 21 | –37 | 74 | 3.65 |
| Paracentral lobule | L | 1 | –9 | –28 | 59 | 3.32 |
| SMA | L | 1 | –6 | –19 | 53 | 3.41 |
| | e. i. R | 3 | 0 | –22 | 65 | 3.40 |
| aPCUN | R | 49 | 15 | –43 | 50 | 4.09 |
| Superior ventral PM | L | 8 | -45 | –10 | 50 | 3.50 |
| | R | 13 | 48 | –1 | 50 | 3.66 |
| SMG | R | 14 | 51 | –19 | 32 | 3.70 |
| CUN | L | | –18 | –67 | –7 | 4.93 |
| STL | L | 1 | –57 | 5 | –10 | 3.55 |
| | R | 71 | 60 | 5 | –10 | 4.03 |
| LG e. i. FG and PHG | L | | –12 | –82 | –13 | 5.72 |
| FG e. i. PHG | R | 29 | 27 | –34 | –16 | 3.97 |

*L, left; R, right; e. i., extending into; MNI, Montreal Neurological Institute; SMA, supplementary motor area; aPCUN, anterior precuneus; PM, premotor cortex; SMG, supramarginal gyrus; CUN, cuneus; STL, superior temporal lobe; PHG, parahippocampal gyrus; LG, lingual gyrus; FG, fusiform gyrus. FDR-corrected at p < 0.01.*

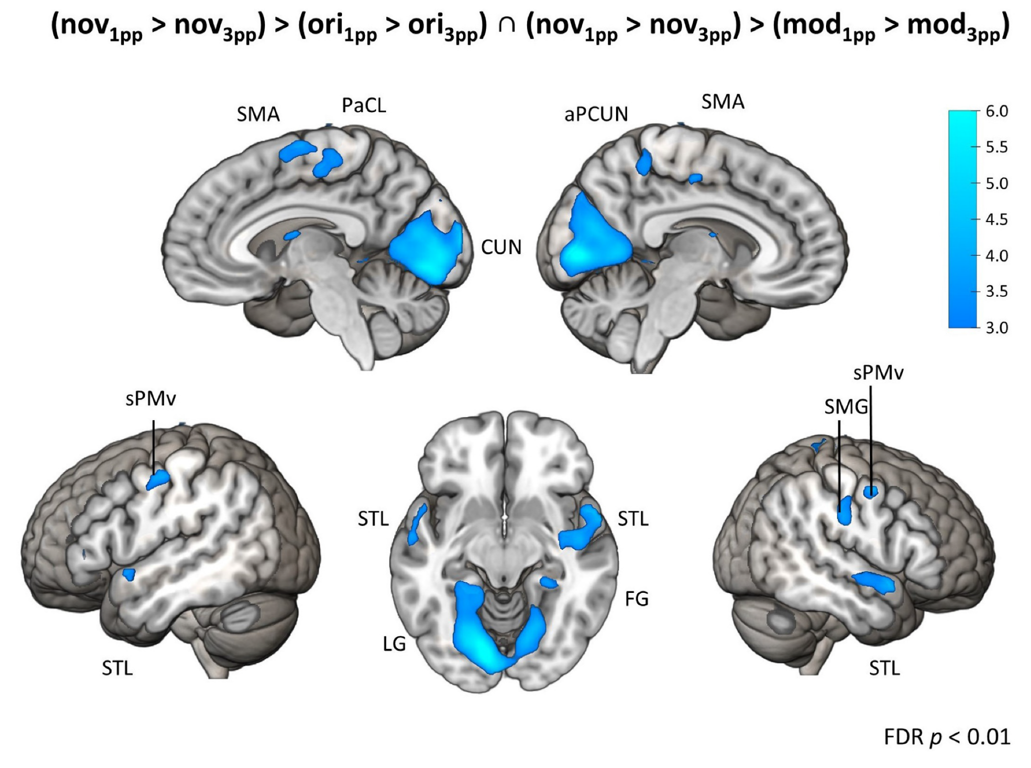

**FIGURE 9 |** Brain activation for perspective. Conjunction contrast showing enhanced brain activity for interaction contrasts of novels vs. original and novels vs. modified versions ($nov_{1pp} > nov_{3pp}$) > ($ori_{1pp} > ori_{3pp}$) ∩ ($nov_{1pp} > nov_{3pp}$) > ($mod_{1pp} > mod_{3pp}$). Activity patterns indicate enhanced activity for a first-person perspective (1pp) compared to a third-person perspective (3pp) for *t*-map at $p < 0.01$ (FDR-corrected). SMA, supplementary motor area; PaCL, paracentral lobule; aPCUN, anterior precuneus; CUN, cuneus; sPMv, superior ventral premotor cortex; STL, superior temporal lobe; LG, lingual gyrus; FG, fusiform gyrus; PoCG, postcentral gyrus.

original versions were presented in the scanner from the 3pp (compared with the 1pp), their modified versions were later more often mistaken for original episodes in the memory test.

## DISCUSSION

Reactivating an episodic memory reinforces its stability (Karpicke and Roediger, 2008), but also allows for the integration of new information, potentially enabling adaptation to an ever-changing world (Lee et al., 2017). Performing an action during encoding and recalling it from one's own perspective are often assumed to support memory retrieval (e.g., Hornstein and Mulligan, 2001; Marcotti and St Jacques, 2018). Therefore, we used subtle breaches of expectation in episodic cueing to test whether active self-performance (vs. passive observation) during encoding and/or first-person (vs. third-person) perspective during re-activation decrease a remembered episode's susceptibility to modification.

Videos reminiscent of previously experienced episodes, in contrast to new videos, triggered an increased BOLD response in a network typical of episodic retrieval (Rugg and Vilberg, 2013; Jeong et al., 2015). Violating expectations of previously experienced episodes triggered an increased BOLD response to modified details in the episodic cues and descriptively prolonged RTs, as described in detail in a separate paper (Siestrup et al., 2021). In line with the here presented activation pattern during episodic retrieval, these findings confirm that subjects had successfully encoded the episodes, which provides the basis for examining the effect of agency during encoding and perspective during retrieval.

When subjects were just attentive observers and not actors themselves during the encoding of episodes, the cue modification and thus the expectation violation triggered a significantly weaker hippocampal response. While there were wide-ranging BOLD effects for 1pp (vs. 3pp) cues that occurred for new videos, these perspective effects were virtually eliminated for episodic cues. As expected, a post-fMRI memory test revealed that episodes presented in a modified version in the scanner were later more often accepted as original episodes in this modified form. Additionally, these modified versions were more often considered new in their original form, especially when presented from 3pp. Together, findings suggest that both agency during encoding and perspective of episodic cueing have a

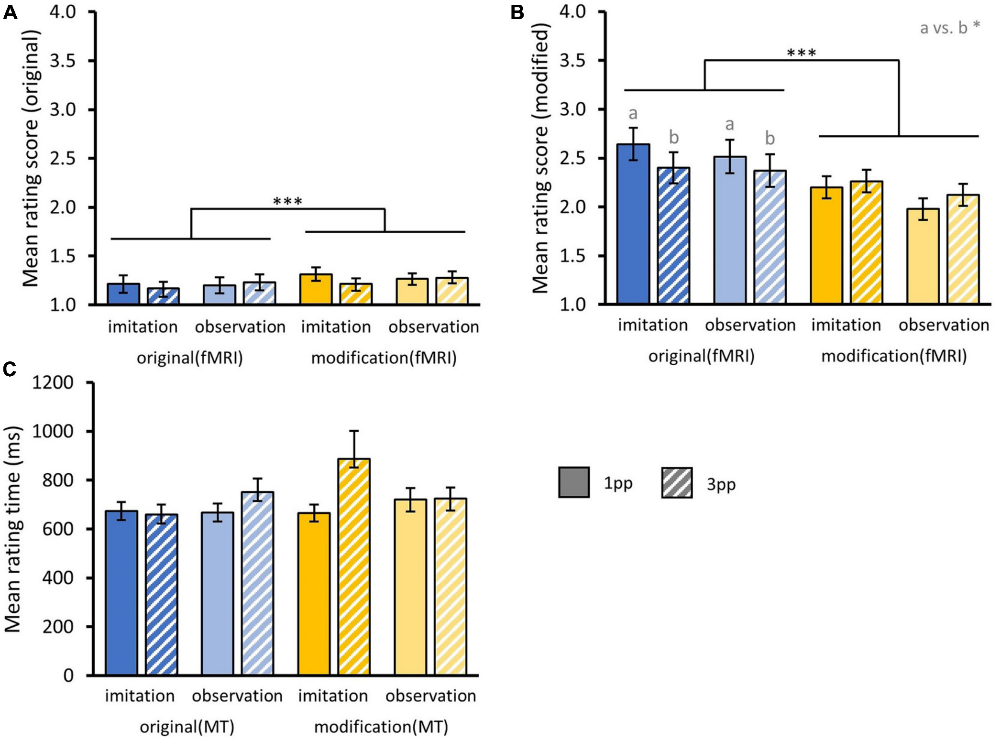

**FIGURE 10** | Behavioral results from post-fMRI memory test. **(A)** Mean rating scores for original and **(B)** modified videos from memory test separated by the factors AGENCY (imitation, observation) and PERSPECTIVE (1pp, 3pp) and fMRI presentation mode MODIFICATION (original, modified). Statistics: rmANOVA based on aligned ranks with *post hoc* paired *t*-tests; a vs. b = $p < 0.05$. **(C)** Overall mean rating times for correct and incorrect responses from memory test. **(A–C)** Bar charts show means and standard errors.

significant effect on episodic memory on the behavioral and the brain level.

## Cerebral Effects of Agency and Cueing Perspective

With regard to the effect of agency, we found a subthreshold effect (uncorrected at $p < 0.001$) of formerly imitated vs. only observed events for manipulated videos. At this level, activity increased in the left posterior PCUN, the frontopolar cortex (BA 10) of the MFC and the left hippocampus, reflecting three areas of the episodic memory network. The precuneus is involved in visuomotor imagery, action planning (Zhang and Li, 2012) and retrieval from long-term memory (Gobbini et al., 2004). Adding to these findings, our fMRI results regarding agency suggest that self-performing compared to only observing may create a stronger internal model of an episode leading to an enhanced prediction error when expectations about the specific episode are violated. As hypothesized, agency specifically affected brain responses to violated, but not to non-violated predictions (brain responses for original videos did not substantially differ on factor levels of agency). Specifically, self-performance may result in deeper encoding by enriching episodes with sensorimotor components, resulting in better retrievable memory traces than mere observation and higher sensitivity to a mismatch between stored and currently perceived information (Manzi and Nigro, 2008; Hainselin et al., 2014; Badinlou et al., 2017).

Previous research suggested that the MFC, specifically BA 10 and ACC, is involved in detecting mismatches between internal model representations and perceived information (Schiffer et al., 2012, 2013). In the present study, we found subthreshold activity in BA 10 for previously self-performed vs. only observed actions during retrieval of modified episodes. Increased activity in BA 10 may point to enhanced episodic success monitoring for previously self-performed vs. merely observed actions (Ramnani and Owen, 2004). Our results may offer an interesting starting point for future research to investigate the role of MFC subregions in processing prediction errors during episodic memory retrieval.

Following our hypotheses, we performed a ROI analysis for the left and right hippocampal complex and found a marginally significant interaction of modification and agency. Exploratory analysis revealed decreased hippocampal activity for modified episodes with a history of observation vs. imitation during encoding in left, but not right hippocampus. Though research showed stronger engagement of left hippocampus regarding the richness of actively self-encoded information

(Rabin et al., 2010), our results on lateralized hippocampal activation have to be interpreted carefully as we had no hypothesis on laterality We take our results as a first indication of hippocampal contribution to expectancy violations of previously self-performed, not merely observed, aspects of an episode. We interpret reduced hippocampal activity as indicative of reduced sensitivity to the detection of episodic expectancy violations in the observation condition. When our internal model fails to predict the current perception, the hippocampus is suggested to generate a mismatch signal (Duncan et al., 2009; Long et al., 2016). Moreover, the hippocampus biases its inherent functional connectivity in response to memory prediction errors, shifting toward encoding of new information and away from retrieval of violated memory-based predictions (Bein et al., 2020). Our findings suggest that the episodic prediction error in hippocampus may be driven by the depth of encoding through a more vivid agentive state, but further validation by future research is necessary. In contrast to previous findings (e.g., Hornstein and Mulligan, 2001), a history of self-performance was ineffective on the behavioral level as self-performed episodes did not lead to better retrieval in the post-fMRI memory test.

Participants were less likely to accept original videos as truly experienced after encountering the modified version, i.e., experiencing a prediction error. While this effect was highly significant, it was small in terms of the absolute rejection rate change. Rather than modifying remembered episodes, prediction errors promoted the learning of new, alternative versions of these episodes, while only slightly alienating the original memories.

Regarding the effects of perspective during episodic memory re-activation, we could not confirm the expected BOLD increase for 1pp vs. 3pp cueing of episodes. Interestingly, contrasting novel videos with previously encountered episodes yielded highly significant effects for 1pp vs. 3pp, including increased activity in the supplementary motor area (SMA), the anterior PCUN, the postcentral gyrus, and areas belonging to the action observation network (AON; Caspers et al., 2010). Potentially, viewing new videos from the 1pp formed a sharp contrast to what the individuals lying in the scanner expected from their own perspective. Seeing an action performed by another person from one's own perspective probably leads to a larger prediction error in the brain than watching that person from an observer perspective, as the former practically never occurs in everyday life. Our fMRI results on cueing perspective show that this strong 1pp effect can disappear when the action is part of our current expectancy repertoire. As participants experienced each story from both perspectives, they presumably encoded episodic memories in a form in which perspective was no longer critical to the generative process of episodic memory retrieval. Other studies reported differential activation for (shifting) perspectives during recall of autobiographical episodic memories (Eich et al., 2009; St Jacques et al., 2017) or during visual imagery (Grol et al., 2017). It is important to note that the type of memory reactivation in the present study differed in various ways from these. Previous studies often used the presentation of pictures or visual imagery to actively trigger episodic memories. By using pictures or verbal cues participants had to recall a scene from a certain point of view or even switch the perspective during retrieval. Thus, memory recall was dependent on the encoding perspective and the ability to mentally visualize an event from a certain perspective. Whether in our study the episodes were encoded in a perspective-neutral manner, or in two distinct variants with different perspectives, is the subject of further experiments.

## Impact of (Not) Maintaining an Episodic Story on Memory Performance

The post-fMRI memory test showed that recurrent re-activation of memories during fMRI resulted in strengthening or distorting subsequent memory performance depending on whether an original or modified video was presented in the scanner. Note that during the post-fMRI test, participants were presented with the scanner version and additionally with a counterpart version of each presented story (i.e., $\text{original}_{\text{fMRI}}$ and $\text{modified}_{\text{MT}}$, or $\text{modified}_{\text{fMRI}}$ and $\text{original}_{\text{MT}}$). After repeatedly re-experiencing a modified video during fMRI, participants showed a lower acceptance for original videos in the post-fMRI test. Note, however, that the absolute decreases in rating scores were small and acceptance rates close to ceiling. Although one could argue here that new information was acquired leading to a bias toward rejecting originals, these results ought to be interpreted with caution.

As expected, after recurrent experience of a modified video during fMRI, participants falsely accepted modified episodes more often as originals. This finding corroborates that prediction errors during episodic retrieval can lead to memory modification (Exton-McGuinness et al., 2015; Sinclair and Barense, 2018). Previous studies suggested that memory content can be overwritten, leading to a loss of previously encoded contents (Lee, 2009). Other studies rather suggest that new information is incorporated into memories, leading to biases or the formation of false memories (Schacter et al., 2011; St Jacques et al., 2013). In line with these latter studies, our results favor additional encoding of false memories, i.e., accepting a modified episode as known from training. A detailed discussion of the effects of modified episodes is provided in Siestrup et al. (2021).

## Influence of Agency and Cueing Perspective on Memory Performance

Previous research showed superior memory performance for episodes in which subjects were agents, not merely observers (Hornstein and Mulligan, 2001; Mulligan and Hornstein, 2003; Leynes and Kakadia, 2013). Considering the assumption that self-referential qualities affect the solidity and re-activation of episodic memory, we expected modified videos of previously self-performed events to be less often incorrectly accepted as known from training.

At a descriptive level, our post-fMRI results showed that previously self-performing (vs. only observing) actions led to better memory performance, irrespective of re-experiencing original or modified episodes during scanning. With regard to our multi-step actions, intensive training and visual accessibility during retrieval, the present study differs from previous studies reporting better memory after self-performance (Hornstein and Mulligan, 2001; Mulligan and Hornstein, 2003). We assume that actively performing and solely observing actions multiple times during training led to equally strong memories of experienced episodes. It has often been reported that observed actions are later remembered as self-performed, a phenomenon called "observation inflation." In this context, it has been suggested that observing actions does also lead to the formation of motor representations, which might be why we could not find an advantage of self-performance for memory stability in the present study (Lindner et al., 2010, 2016; Leynes and Kakadia, 2013).

Episodes recalled from the 1pp perspective are generally remembered better than those recalled from the 3pp perspective (Rice and Rubin, 2009; Akhtar et al., 2017; Marcotti and St Jacques, 2018). Thus, we expected lower false memory scores (i.e., modified episodes incorrectly classified as known from training) when videos corresponded to original episodes cued from 1pp during fMRI. As expected, participants less often accepted a modified video when they encountered original counterparts in the 1pp (vs. 3pp) during fMRI, speaking in favor of a subtle perspective effect on episodic retrieval. Previous research explains such benefits by a more detailed and vivid recall of a truly experienced episode during 1pp retrieval (Rice and Rubin, 2009; Marcotti and St Jacques, 2018) and by greater availability of visual information (Libby and Eibach, 2011; Butler et al., 2016). In the present study, the latter explanation can be ruled out, since perspective of episodic cues was manipulated only by a 180° rotation. Thus, our results suggest that cueing videos from the observer perspective affected the detectability of modifications rather than the accessibility of stored visual information during retrieval. Accordingly, participants were more likely to detect changes in the post-fMRI memory test presumably because field perspective allows subjects to focus their attention more on specific features of a remembered event (Libby and Eibach, 2011). This is further corroborated by faster recognition of actions presented from 1pp vs. 3pp during fMRI.

## CONCLUSION

Self-referential factors, such as agency during encoding and perspective during retrieval, are suggested to shape episodic memories. The present study used episodic prediction errors to test whether or not these self-referential factors inhibit or promote the error-induced change of episodic memories, and to examine the brain processes underlying these changes. The hippocampal response was reduced to episodic prediction errors when subjects had encoded episodes only as observers. Thus, predictions derived from episodic memories based on self-performed actions might be stronger than those based on only observed actions. However, this effect was not reflected in post-fMRI memory performance. In contrast, repeated retrieval of encoded episodes from 3pp resulted in more false memories. In summary, the robust response to episodic prediction errors was subtly modulated by agency during encoding and by perspective during retrieval of episodic memory. Both factors may therefore also be relevant to the question of whether and how much is learned from episodic prediction errors. This could become the starting point for further investigations.

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Ethics Committee of the Department of Psychology, University of Münster. The patients/participants provided their written informed consent to participate in this study.

## AUTHOR CONTRIBUTIONS

BJ, SS, NE-S, and RS contributed to conception and design of the study. BJ performed the statistical analysis and wrote the first draft of the manuscript. RS wrote sections of the manuscript and contributed with scientific support, supervision, and coordination. IT and SS provided substantial help with the data analysis. All the authors contributed to manuscript revision, read, and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnbeh.2021.793115/full#supplementary-material

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## 3.2 Study 2: Solidity Meets Surprise: Cerebral and Behavioral Effects of Learning from Episodic Prediction Errors

Running title: Learning from Episodic Prediction Errors

Sophie Siestrup, Benjamin Jainta, Sen Cheng, & Ricarda I. Schubotz (2023)

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# Solidity Meets Surprise: Cerebral and Behavioral Effects of Learning from Episodic Prediction Errors

**Sophie Siestrup**[1,2*], **Benjamin Jainta**[1*], **Sen Cheng**[3], and **Ricarda I. Schubotz**[1,2]

## Abstract

■ How susceptible a memory is to later modification might depend on how stable the episode has been encoded. This stability was proposed to increase when retrieving information more (vs. less) often and in a spaced (vs. massed) practice. Using fMRI, we examined the effects of these different pre-fMRI retrieval protocols on the subsequent propensity to learn from episodic prediction errors. After encoding a set of different action stories, participants came back for two pre-fMRI retrieval sessions in which they encountered original episodes either two or eight times in either a spaced or a massed retrieval protocol. One week later, we cued episodic retrieval during the fMRI session by using original or modified videos of encoded action stories. Recurrent experience of modified episodes was associated with increasing activity in the episodic memory network including hippocampal and cortical areas, when leading to false memories in a post-fMRI memory test. While this observation clearly demonstrated learning from episodic prediction errors, we found no evidence for a modulatory effect of the different retrieval protocols. As expected, the benefit of retrieving an episode more often was reflected in better memory for originally encoded episodes. In addition, frontal activity increased for episodic prediction errors when episodes had been less frequently retrieved pre-fMRI. A history of spaced versus massed retrieval was associated with increased activation throughout the episodic memory network, with no significant effect on behavioral performance. Our findings show that episodic prediction errors led to false memories. The history of different retrieval protocols was reflected in memory performance and brain responses to episodic prediction errors, but did not interact with the brain's episodic learning response. ■

## INTRODUCTION

Through episodic memories, we can mentally relive events from our personal past (Tulving, 2002), and yet, episodic memories are not always veridical reconstructions of our experiences (Scully & Hupbach, 2020; Lee, Nader, & Schiller, 2017; Nader, 2015; Nader & Einarsson, 2010). In everyday life, there is always a certain discrepancy between our expectations, which we derive from memories, and new experiences. According to the predictive coding framework, this discrepancy gives rise to prediction errors, which serve as bottom–up learning signals to the brain (Reichardt, Polner, & Simor, 2020; Barto, Mirolli, & Baldassarre, 2013). It has been suggested that memory modification is fueled by mnemonic prediction errors (Sinclair & Barense, 2018; Fernández, Boccia, & Pedreira, 2016), that is, subtle discrepancies between the remembered situation and the current situation that are encountered during retrieval. Memory modification could be functional in that it allows us to maintain valid predictions in a highly dynamic environment. Thus, new experiences can be integrated into existing memories or *internal models* (Barron, Auksztulewicz, & Friston, 2020) to successfully guide our behavior in the long run (Fernández et al., 2016; Exton-McGuinness, Lee, & Reichelt, 2015).

In the current fMRI study, we examined the influence of different episodic memory retrieval protocols on learning from mnemonic prediction errors. To this end, we used an episode-modification paradigm adapted from our previous study (Jainta et al., 2022). First, participants went through a training during which they encoded episodes. Then, they completed two active pre-fMRI retrieval sessions. Half of the episodes were retrieved in a spaced schedule, that is, during both sessions, whereas the other half was retrieved in a massed schedule, that is, only in the second session. Overall, half of the episodes were retrieved only two times, whereas the other half were retrieved eight times. During the subsequent fMRI session, participants were presented videos reminiscent of the encoded episodes. Whereas some episode videos were presented in their original form, others were manipulated to induce prediction errors. Finally, participants completed a post-fMRI memory test that queried their memory of episodes originally experienced.

A fundamental factor mediating memory solidity is consolidation, a process that stabilizes a memory trace after its initial encoding. It occurs not only during sleep because of off-line replay (Poe, Walsh, & Bjorness, 2010), but also

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[1] University of Münster, Germany, [2] Otto Creutzfeldt Center for Cognitive and Behavioral Neuroscience, University of Münster, Germany, [3] Ruhr University Bochum, Germany

*These authors contributed equally and share first authorship.

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when a memory is actively retrieved (Antony, Ferreira, Norman, & Wimber, 2017). Retrieval practice does not only improve memory performance, establishing the so-called "testing effect" (Rowland, 2014), but can also protect memories from later modification (Elsey, Van Ast, & Kindt, 2018; Antony et al., 2017). On the one hand, memory performance improves when an item is practiced more often (Lyle, Bego, Hopkins, Hieb, & Ralston, 2020; Karpicke & Roediger, 2007; Underwood, 1970). On the other hand, spreading the information to be practiced over several repetitions, so-called spaced practice, is more efficient for long-term retention than practicing all items on a single occasion, called massed practice (Lyle et al., 2020; YeckehZaare, Resnick, & Ericson, 2019; Kang, 2016; Gerbier & Toppino, 2015; Dempster, 1989; Underwood, 1970). The positive effect of spaced practice has been explained by more effortful preretrieval processing (Feng et al., 2019; Dobson, Perez, & Linderholm, 2017) that determines later retrieval success (Rowland, 2014). Against this backdrop, we expected that spaced (vs. massed) retrieval of episodic memories as well as retrieving them more (vs. less) frequently would lead to particularly stable memory traces, which should render episodic memories less susceptible to later change.

First, we tested the behavioral hypothesis that more consolidated episodes would be less susceptible to change during retrieval. As previously reported (Jainta et al., 2022; Siestrup et al., 2022), we found that repeated prediction violation leads to increased acceptance of modified episode videos as originally encoded, and decreased acceptance for unmodified videos, corroborating the idea that mnemonic prediction errors can contribute to memory modification. The behavioral data suggested that this modification consisted of incorporating additional variants of the episode rather than overwriting the original episode. Building on this observation, we now tested whether this learning process depends on the solidity of memory, which we manipulated using different retrieval protocols. In particular, we expected that modified videos of more solid episodes, that is, those that were retrieved more frequently and/or following a spaced protocol, would not be as readily accepted as original as modified videos of less solid ones (Schiffer, Ahlheim, Ulrichs, & Schubotz, 2013).

Second, using fMRI, we aimed to elucidate the neural processes underlying learning from episodic prediction errors. Previous studies found elevated activation in the hippocampal formation and medial frontal cortex (FMC) during the recall of supposedly more consolidated memories (Bosshardt et al., 2005), either because of more frequent prior retrieval (Wiklund-Hörnqvist, Stillesjö, Andersson, Jonsson, & Nyberg, 2021; Schiffer et al., 2013) or a spaced retrieval schedule (Li & Yang, 2020; Ezzyat, Inhoff, & Davachi, 2018; Zhan, Guo, Chen, & Yang, 2018; Takashima et al., 2009). On the basis of own previous studies, we expected that the moment of modification in an episodic cue triggers increases activity in areas that process mnemonic prediction errors (Schiffer et al., 2013; Schiffer, Ahlheim, Wurm, & Schubotz, 2012). We especially addressed the role of two brain areas, the hippocampal formation and the FMC, in learning from prediction errors during retrieval of differently consolidated episodes, as previously suggested (Bein, Duncan, & Davachi, 2020; van Kesteren, Ruiter, Fernández, & Henson, 2012). The hippocampus is known to be relevant for both associative learning (Suzuki, 2007) and initial consolidation through its link to neocortical areas (Squire, Genzel, Wixted, & Morris, 2015). Presumably because of this dual function, the hippocampus mediates the comparison of new information with stored memories, which may lead to an updating of the internal model (Long, Lee, & Kuhl, 2016; Duncan, Curtis, & Davachi, 2009; Kumaran & Maguire, 2007). The FMC is thought to play a more general role in the retrieval of consolidated memories (Preston & Eichenbaum, 2013; Sterpenich et al., 2009; Takashima et al., 2009). Against this background, we expected that the hippocampal complex (HC) and FMC respond more strongly to mnemonic prediction errors when more solid memories are involved, as divergent information triggers stronger mismatch signals for more consolidated memory traces (Schiffer et al., 2012, 2013).

However, it is also possible that less stable memories might be more difficult to retrieve and thus lead to higher activation in areas that are typically involved in episodic retrieval (e.g., Nadel, Campbell, & Ryan, 2007), including the hippocampus and FMC. Accordingly, it could be that neural prediction error signals are stronger for weaker memories, resulting in higher learning rates. To account for both options, we examined all effects for both supposedly strongly versus weakly consolidated memories and vice versa. Together with the behavioral findings, we would then be able to make assumptions about how learning from episodic prediction errors is accomplished by the brain.

As an important final step, we aimed at combining our functional and behavioral measures to investigate which neuronal processes give rise to learning from prediction errors, and how they might interact with memory solidity. In principle, learning from prediction errors can include two different phenomena (Gershman, Monfils, Norman, & Niv, 2017). In that sense, one possibility is that prediction errors could lead to a modification of old memory traces. In the memory test, this would manifest through more false negatives (misses). Alternatively, prediction errors might drive the acquisition of alternative variants of earlier memories, which would result in more false positives (false alarms). Because we observed high hit rates (i.e., low miss rates) combined with high false alarms rates in our previous study (Jainta et al., 2022), we sought here to test which brain areas reflect a gradual establishment of false memories. There is evidence suggesting increased hippocampal activity during successful encoding (Davachi, Mitchell, & Wagner, 2003) and retrieval of episodic information while activation decreases with familiarity (Yonelinas, Otten, Shaw, & Rugg, 2005). In addition, stronger hippocampus activity during encoding is associated with better episodic memory (Davachi, 2006). Previous studies have shown that episodic memory encoding is characterized by increasing neocortical activity and decreasing hippocampal activity with number of repetitions (Brodt et al., 2016, 2018) and also with ongoing consolidation (Takashima et al., 2006). However, no studies have yet examined the cerebral reflection of incremental learning because of repeated episodic prediction errors. Hence, we were specifically interested in the dynamic increase of brain responses with accumulating evidence for new episode "alternatives." We expected that brain activity increases in areas related to memory formation, including hippocampal and parahippocampal regions (Ritchey, Libby, & Ranganath, 2015).

## METHODS

This article is based on experimental data that were previously published in a companion paper (Siestrup et al., 2022). Please note that the factors addressed in this article were statistically independent of those reported in the companion paper.

### Participants

Forty-five participants took part in the study. Like in our previous study (Jainta et al., 2022), participants were all female to achieve a good match between the hands in the videos and the hands of the participants. This was important for the credibility of our cover story that participants would be presented videos of themselves during the fMRI session. Four participants started the experiment but did not finish, either because of technical problems during the second retrieval session (three participants) or personal reasons (one participant). Data from five additional participants were excluded from analyses because of the incorrect presentation of video stimuli during the fMRI session (one participant) and increased movement during the fMRI session (four participants, approx. 5-mm movement). Consequently, 36 participants were part of the final sample ($M$ = 22 years, $SD$ = 2.78 years, range = 18–30 years). This sample size yielded stable results in our previous work, where we used not only the same number of participants but also an equivalent experimental and statistical design with the same number of conditions and trials (e.g., Jainta et al., 2022).

Participants had (corrected-to-) normal vision, were native German speakers, were and right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). They reported no history of neurological or psychiatric disorders or substance abuse. Participants received course credits or money for their participation and gave written informed consent to participate in this study. The study was conducted in accordance with the Declaration of Helsinki and approved by the local ethics committee of the University of Münster.

### Stimuli

We used the same set of videos as previously reported (Jainta et al., 2022; available upon request at https://www.uni-muenster.de/IVV5PSY/AvicomSrv/). These were 78 short films (duration = 8.80–17.88 sec, $M$ = 12.71 sec; six to nine action steps, $M$ = 7.4 steps) showing stories played with PLAYMOBIL toys from a first-person perspective. Videos depicted toys from above being manipulated in front of a matte white background and the hands and underarms of an actress wearing a black pullover and black gloves. The back of the right hand was additionally marked with a yellow dot to facilitate imitation from demo videos (Franz, Ford, & Werner, 2007). Videos were filmed with a digital single-lens reflex camera (Nikon D5300). The section captured by the camera (47.5 cm × 28 cm; in the following referred to as camera frame) was marked on the background with tape. For each video, objects that were needed for the story were placed next to the camera frame and moved into view when they first appeared in the story. For editing video material, we used Adobe Premiere Pro CC (Adobe Systems Software, Version 12.1.2). Videos were cut so that they started with seven frames of white background and ended after seven frames of the final toy constellation. The frame size of the videos was 1920 × 1080 pixels, and the frame rate was 25 frames per second. Videos were presented at a visual angle of approximately 7.3° × 13° with the stimulus presentation software Presentation (Version 20.3 02.25.19, Neuro-Behavioral Systems) throughout the study.

A subset of 24 stories existed in three different versions. First, there was an original version (*ori*), which was used for encoding and retrieval. Second, in a modified version of the story, two adjacent action steps were switched (structure modification) to elicit prediction errors based on episode structure (*str*). Third, one object was exchanged as compared with the original version of the story (content modification) to elicit prediction errors based on episode content (*con*). Modifications did not occur during the first two or last two action steps. Effects regarding the factor modification (*str*, *con*) were addressed in a companion paper (Siestrup et al., 2022). In this article, we aggregated the modified videos (*str*, *con*) and will refer to them as modified versions (*mod*) in the following sections. Four additional videos were first introduced in the fMRI session and will be referred to as novels in the following. Two more videos were used for practice trials for the different tasks and were not shown in the fMRI experiment. These six videos existed in only one version each.

### Procedure

For an overview of the procedure, please see Figure 1.

#### *Encoding*

For encoding of episodes, participants went through two initial training sessions in a computer lab at the

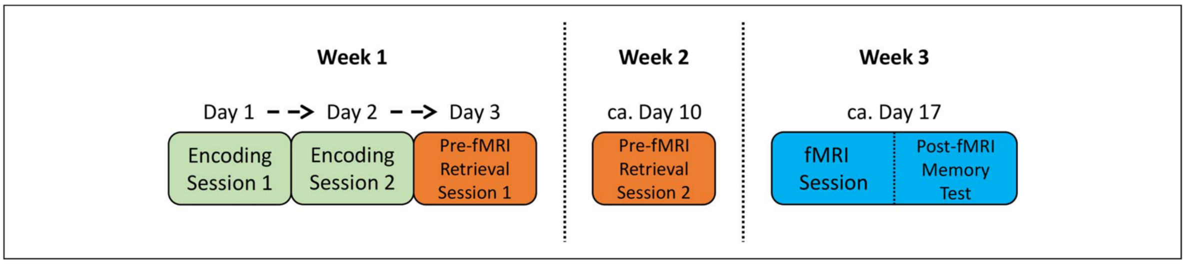

**Figure 1.** Schematic overview of the experimental procedure. During the first week, participants underwent two encoding sessions and one pre-fMRI retrieval session on three consecutive days. The first retrieval session only contained videos belonging to the spaced condition. Approximately 1 week later, participants returned to the behavioral laboratory for the second pre-fMRI retrieval session, during which they re-encountered videos belonging to the spaced as well as the massed condition. In Week 3, participants came back for the fMRI session, which was immediately followed by a post-fMRI memory test about which participants were not informed beforehand.

Department of Psychology at the University of Münster. The two sessions were conducted on two consecutive days and lasted about 2.25 and 1.75 hr, respectively, and during each session, participants encoded half of the 24 episodes.

Before the first encoding session started, participants were informed that their hands and forearms will be filmed to use these videos for the fMRI session (cover story). In contrast to our previous study, participants now imitated all of the 24 stories from demo videos (i.e., the original versions). For that, each video was presented three times in the first-person perspective (1 pp) and, afterward, had to be imitated correctly three additional times by the participant. For each participant, the order of videos was randomized. All stories were equally often encoded during the first and second sessions over the course of the study. Videos trained during Sessions 1 and 2 were balanced for the number of action steps.

During encoding sessions, participants wore the same black pullover and gloves as the actress when filming the demo videos and sat at the same filming setup. This way, the hands and arms of participants closely resembled those of the original actress in the videos, which was important for our cover story that participants would be presented videos of themselves during the fMRI session. The experimenter was present to monitor the participants' performance via a monitor that provided a live view of the participants' actions (Figure 2). Before a new video was shown, all toys included in the story were placed next to the camera frame in the same way as during the creation of the stimulus material. After three correct imitations of the story as judged by the experimenter, participants had to describe the story in detail to ensure that they had paid attention to all objects and had understood the story correctly. The experimenter immediately interrupted the participants as soon as they made a mistake during an imitation or description attempt to avoid encoding of wrong stories. In both cases, the experimenter then corrected the participant who had to start with a new imitation/description attempt. The experimenter monitored all details of the story as closely as possible, including the sequence of action steps and the correct positioning of hands and objects. Participants only performed one incorrect imitation attempt, on average ($M$ = 1.037, $SD$ = 0.469), so that they needed, on average, four attempts to complete the three correct imitations.

### *Pre-fMRI Retrieval Sessions*

To further consolidate episodic memories, the second phase of the study was active retrieval of the before encoded stories. To this end, participants went through two pre-fMRI retrieval sessions. The first retrieval session took place 1 day after the second encoding session, the second retrieval session was conducted approximately 1 week later (range = 4–8 days; $M$ = 6.36 days, $SD$ = 0.93 days). Both sessions were conducted in a computer laboratory at the Department of Psychology at the University of Münster.

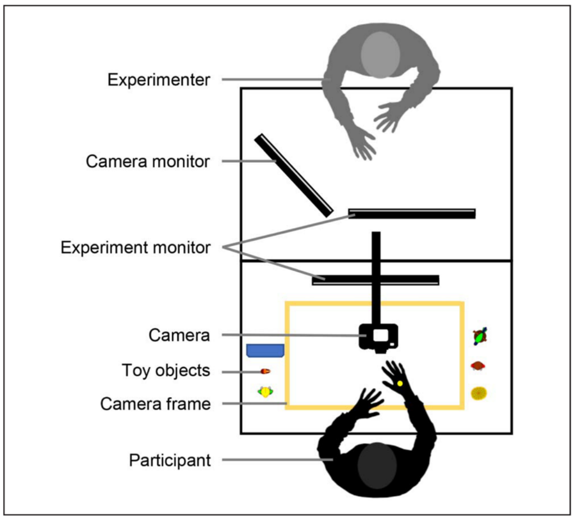

**Figure 2.** Encoding setup. During training, participants imitated PLAYMOBIL stories, while sitting at the filming setup. Their performance was monitored by the experimenter. Figure adapted from Siestrup et al. (2022).

During the retrieval task, participants always saw the first two steps of a demo video. Then, the video stopped and a question was displayed, which was either “Left?” or “Right?” Participants were instructed to visualize the rest of the story from memory and then answer how many steps of the entire story had been played with the left or right hand, respectively. Participants had to answer by pressing a number key (0–9) on their keyboard. We chose this approach because we wanted to encourage active retrieval of the encoded episodes without laying a special focus on aspects that would be modified during the fMRI session. Thus, we wanted to avoid asking for specific contents or steps involved in the actions. In addition, we chose this question because it could not be answered with mere gist-knowledge about the episode. Importantly, the number of steps that were conducted with the left or right hand did not change in videos containing either type of modification. Upon response delivery, the video played until the end. Participants were instructed to carefully watch the video to self-check their answers. Afterward, written feedback (“correct,” “incorrect”) was displayed on the screen for 1.5 sec. When feedback is included in retrieval tasks, consolidation has been shown to occur irrespective of the initial retrieval success (Rowland, 2014; Roediger & Butler, 2011). The task was self-paced, so participants could decide themselves when they wanted to proceed with the next video. As videos were not only presented once but several times (outlined below), participants were explicitly instructed to always visualize the story and not just remember previous responses they gave. Each type of question was presented equally often after each video and per session. For a schematic depiction of the retrieval task, see Figure 3.

Half of the stories were retrieved two times, the other half eight times (factor TIMES). Furthermore, half of the stories were retrieved during two separate sessions, that is, in a spaced manner, whereas the other half of the stories were retrieved only in Session 2, that is, in a massed manner (factor SCHEDULE). All episodes that were retrieved in a spaced manner were trained in Session 1 either 1 or 4 times, depending on which factor level of TIMES they belonged to. Therefore, the retrieval task comprised 30 trials (plus two practice trials) in Session 1. The remaining repetitions, so either one our four additional trials per story, were conducted in Session 2 (30 trials). In addition, all episodes that were retrieved in a massed way were trained in Session 2 (60 trials). Thus, the retrieval task in Session 2 comprised 90 trials in total. Trials of different levels of the factor SCHEDULE (*spaced, massed*) were not trained in an interleaved manner to keep the second retrieval of spaced items comparable to the first. Instead, trials were blocked according to the factor level of SCHEDULE. Order of spaced and massed blocks was counterbalanced between participants. Within blocks, videos were trained in a pseudorandom order. Repetitions of the same video were also blocked together to avoid additional spacing effects on a trial basis.

To avoid additional practicing between pre-fMRI retrieval sessions, participants were informed that they would perform a similar, but different task in Session 2 and explicitly asked not to think about the episodes between experimental sessions. To control for additional practice, participants were asked at the end of each session whether they had tried to actively remember the videos before the session. None of the participants reported to have visualized the episodes outside the laboratory. At the end of Session 2, participants went through a short practice (four video trials, four question trials, one null event) of the task they would conduct during the fMRI scan. Please note that participants were informed during

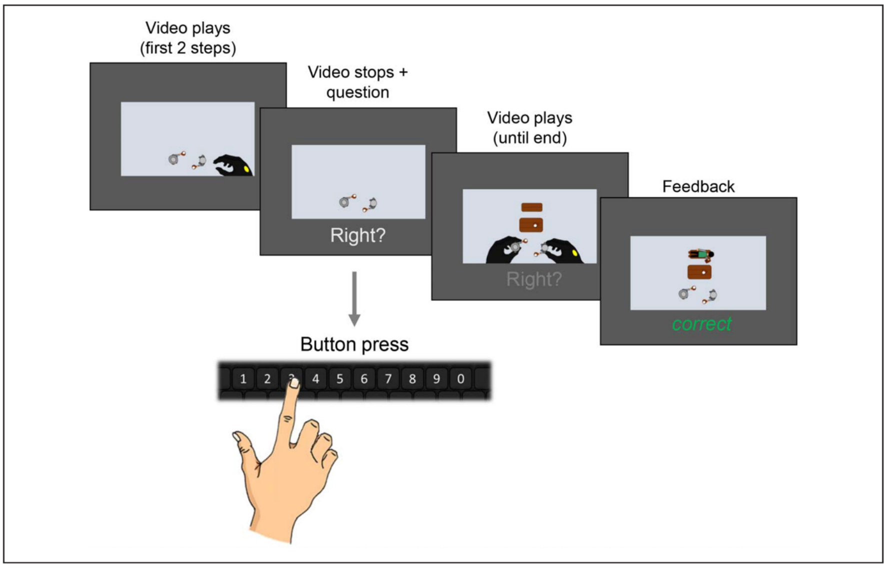

**Figure 3.** Schematic depiction of retrieval task. Participants were presented the first two steps of a demo video. Then, the video stopped and a question (“Left?” or “Right?”) was displayed. Participants had to visualize the story from memory and answer how many steps were conducted with the left or right hand, respectively, using the number keys on their keyboard. Upon response delivery, the video proceeded to play until the end, and written feedback was provided (“correct” or “incorrect”). The task was self-paced. Because of copyright restrictions, we show schematic illustrations of the stimulus material.

the first encoding session that they will be presented with videos of their own during the fMRI session. Therefore, participants were aware from the beginning on that they would re-encounter the encoded action stories again.

### *fMRI Session*

The fMRI session was conducted approximately 1 week after the second pre-fMRI retrieval session (range = 6–13 days; *M* = 7.69 days, *SD* = 1.31 days). Participants were presented with original and modified videos similar to the previously encoded and retrieved episodes. As in our previous study (Jainta et al., 2022), participants were told that videos of themselves playing the stories would be presented in the fMRI session. However, this was only a cover story to elevate personal identification with the videos to benefit episode reactivation. In fact, participants were never presented videos of themselves. They were fully debriefed after completing the experiment.

Each story was only shown in the original (eight videos) or one divergent form (structure or content modification; eight videos each). Before the fMRI session, stories had either been retrieved two or eight times and the total number of retrieval times had either been spaced out over the two pre-fMRI retrieval sessions or massed together in Session 2. Videos were allocated to conditions pseudorandomly so that individual videos belonged to each condition minimally two and maximally six times (3 times on average) over the course of the experiment. In addition, four novel stories were included in the fMRI session.

The fMRI experiment was divided into six blocks, each containing the 24 videos that had been previously encoded during the training sessions. Each of these 24 episodes was either presented in an original or a slightly modified version once per block and, thus, was repeated six times in total over the course of the fMRI session. Over the entire experiment, the trial order was pseudorandomized and transition probabilities were checked to ensure a balanced number of transitions between conditions. Therefore, we ensured each condition followed every other condition, including the same condition, equally often. Each block in addition contained three null events (fixation cross for 7 to 10 s) and four completely new videos (i.e., novels), leading to 18 null events and 24 novel video trials in the whole session.

During the fMRI session, the participants' task was to attentively watch the videos and answer a question after some video trials. The task was included to focus the participants' attention on the video stimuli, as applied in previous studies (Jainta et al., 2022; El-Sourani, Trempler, Wurm, Fink, & Schubotz, 2019). Questions were short descriptions (e.g., "Rescuing princess?") of stories and the participants had to indicate whether this description matched or did not match the previously displayed video. To do so, they had to press one of two buttons on a response box with the right index finger (yes) or middle finger (no), respectively (Figure 4). Question trials were pseudorandomly interspersed with video trials. Over the course of the experiment, each story (including novels) was once followed by a matching, once by a non-matching description. Thus, there were 56 question trials in total.

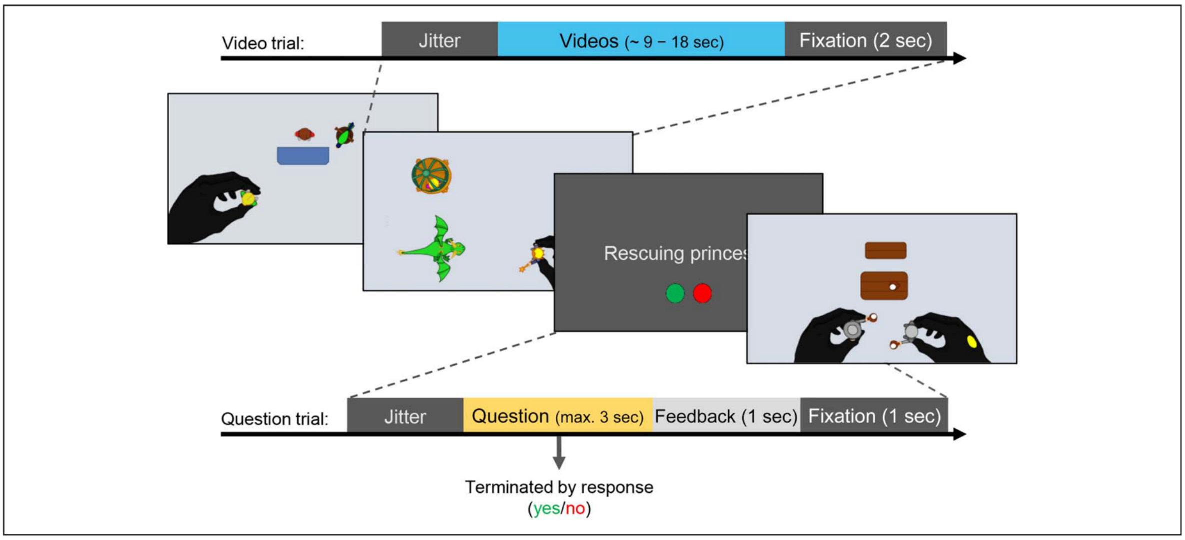

**Figure 4.** Schematic depiction of task during fMRI session. Video trials included a variable jitter (0, 0.5, 1, or 1.5 sec of fixation), a video showing a PLAYMOBIL story (ca. 9–18 sec), and a 2-sec ISI (fixation). Question trials consisted of a variable jitter, a question regarding the story shown in the preceding video (terminated by response or maximally 3 sec long), and a 2-sec ISI. The ISI after question trials was divided into a 1-sec feedback ("correct," "incorrect," "too late") and a 1-sec fixation. Under the question text, it was shown which button should be pressed to accept (left, green) or reject (right, red) the description.

Each block contained 9 to 10 question trials to achieve an approximately even distribution of question trials over the experiment. Maximally two successive videos were followed by questions. Like that, we aimed to ensure that question trials were neither highly irregular nor highly predictable so that participants would have to stay attentive at all times. Questions were presented for maximally three seconds or until participants responded. Participants then received one second of written feedback whether they had answered correctly, incorrectly or too late, in case no response was given.

During ISIs, a fixation cross was presented (duration: 2 sec, 1 sec after question trials). In addition, a variable jitter of 0, 0.5, 1 or 1.5 sec of fixation was added between trials for enhancement of the temporal resolution of the BOLD response (Figure 4). The fMRI task had a total duration of approximately 48 minutes.

### *Post-fMRI Memory Test*

The memory test was conducted as previously described (Jainta et al., 2022). Participants were not informed that their memory for episodes would be tested at the end of the experiment.

Immediately after the fMRI session, participants were seated in a separate room in front of a laptop and instructed to remember their encoding sessions. The stories that had been part of the fMRI were now presented in two different versions. When during the fMRI experiment, an original version of a story had been presented, this was now presented as well. Half of these stories were then additionally presented in a structure-modified version, the other half in the content-modified version. When a modified version had been presented in the scanner already, stories were presented in the same modified version as well, and additionally in the original version. Novel videos which had been encountered during the fMRI session for the first time were now presented twice in the same version to keep the number of presentations per action story equal for all conditions. Importantly, participants were not explicitly informed that modified and novel videos would be presented. The video presentation order was pseudorandomized, so that half of the stories (of each experimental condition) were first presented in a modified version followed by an original version and vice versa. Importantly, videos depicting alternative versions of the same story were not shown in direct succession.

The participants' task was to rate after each video whether they knew this exact episode from the encoding sessions, using a Likert scale including 1 (yes), 2 (rather yes), 3 (rather no) and 4 (no). Answers were collected via four marked keys on the laptop's keyboard. Please note that for the analysis of ratings, we reversed the coding of responses, so that higher ratings indicate higher acceptance. Response time was unrestricted, but participants were instructed to react quickly and intuitively. In total, the memory test comprised 56 video trials and the completion of the task took approximately 15 min.

## MRI Data Acquisition and Preprocessing

MRI scans were acquired with a 3-Tesla Siemens Magnetom Prisma MR tomograph and a 20-channel head coil. Participants lay on the scanner bed in a supine position, their index and middle finger positioned on the two buttons on the response box. Movements of the head and arms were minimized by fixation with form-fitting cushions. During the scan, participants wore earplugs and headphone to attenuate scanner noise. Stimuli were projected on a screen behind the fMRI machine which participants saw through an individually adjusted mirror on the head coil.

Before functional imaging, high-resolution anatomical images (T1 weighted) were created with a 3-D multiplanar rapidly acquired gradient-echo sequence (192 slices, voxel size = 1 $mm^3$, repetition time = 2130 msec, echo time = 2.28 msec, flip angle = 8°, field of view = 256 × 256 $mm^2$). Functional images were acquired in interleaved order along the AC–PC plane using a gradient-echo EPI sequence to measure BOLD contrast (33 slices, voxel size = 3 $mm^3$, repetition time = 2000 msec, echo time = 30 msec, flip angle = 90°, field of view = 192 × 192 $mm^2$).

Imaging data were processed with SPM12 (Wellcome Trust) implemented in MATLAB (Version R2020b, The MathWorks Inc.). We applied slice time correction to the middle slice, movement correction and realignment to the mean image, co-registration of functional to structural scans, normalization of functional and structural images into standard Montreal Neurological Institute (MNI) space, and spatial smoothing using a Gaussian kernel of FWHM of 8 mm. A 128-sec high-pass temporal filter was applied.

## Statistical Data Analysis

### *Behavioral Data Analysis*

The behavioral data analysis was conducted with RStudio (R Core Team, 2020; Version 1.3.1073).

To analyze the participants' performance during the pre-fMRI retrieval sessions, we applied a 2 × 2 within-subject factorial design. Factors were retrieval TIMES (*8*, *2*) and SCHEDULE (*spaced*, *massed*), and we calculated the correct answer rate for all factorial combinations collapsed over both retrieval sessions.

For analyzing data from the fMRI session and post-fMRI memory test, we applied a 2 × 2 × 2 within-subject factorial design. Factors were retrieval TIMES (*8*, *2*), SCHEDULE (*spaced*, *massed*), and $\text{MODIFICATION}_{\text{FMRI}}$ (*no*, *yes*). For the analysis of behavioral performance during the fMRI session, we first excluded those 0.2% of question trials during which no answer was given. We then calculated the error rate and mean RT (including only correct responses) for each factorial combination.

For the analysis of data collected during the post-fMRI memory test, we analyzed responses to modified (in memory test) and unmodified (in memory test) videos separately, in the following referred to as modified$_{\text{MT}}$ and unmodified$_{\text{MT}}$. For each factorial combination, we calculated the mean rating score. Please note that for this analysis, we reversed the initial coding of responses as it is more intuitive that higher scores indicate higher acceptance. In addition, we calculated the mean RTs (correct responses only) for each factorial combination. RTs can be used as indicators of how long it takes to retrieve information (correctly) from memory (Collins & Quillian, 1969). Longer RTs can be interpreted as increased difficulty of retrieval because of elevated cognitive processing demands (Noppeney & Price, 2004; Larsen & Plunkett, 1987), which may also occur when competing versions of an episode are processed. As some participants did not give any correct answers for some factorial combinations, the sample size for the analysis of RTs was reduced to 35 (unmodified$_{\text{MT}}$) and 23 (modified$_{\text{MT}}$) participants.

For all behavioral analyses, we applied a significance level of $\alpha = .05$. Data were inspected for normal distribution with the Shapiro Wilk Test and checked for outliers as defined as values higher than the 75% quartile $+3 \times$ interquartile range or lower than the 25% quartile $-3 \times$ interquartile range. When data were normally distributed or could be transformed to fit normal distribution (RTs; logarithmic transformation) and showed no extreme outliers, we employed a three-way repeated-measures analyses of variance (rmANOVA). When the prerequisites for parametric analysis were not met, we used a nonparametric three-way rmANOVA based on aligned rank data (package *ARTool*; Wobbrock, Findlater, Gergle, & Higgins, 2011) and computed post hoc pairwise comparisons using the Wilcoxon signed-ranks test (one-tailed with respect to our hypotheses). *p* Values were adjusted according to the Bonferroni correction for multiple comparisons (Bonferroni, 1936). As descriptive statistics, we report mean values and standard errors of the means.

### *fMRI Design Specifications*

For the analysis of fMRI data with SPM12, we used general linear models (GLM) for serially autocorrelated observations (Worsley & Friston, 1995; Friston et al., 1994). We set up four different GLMs, in each of which the six subject-specific rigid-body transformations obtained from realignment were included as regressors of no interest. All regressors were convolved with a canonical hemodynamic response function.

We applied gray matter masking on the first level of all analyses, by using the smoothed individual normalized gray matter image (8-mm FWHM), thresholded at .2 using ImCalc in SPM12, as a binary mask (https://jpeelle.net/mri/misc/creating_explicit_mask.html). Second-level group analyses were performed with one-sample *t* tests across participants. To control for false positive results, we applied false discovery rate (FDR) correction and a threshold of $p < .05$ or higher (voxel level) to resulting *t*-maps. For completeness of our analysis and with regard to our hypotheses, when no significant activation could be detected using this threshold, we applied a threshold of $p < .001$ (uncorrected) and included the results in the Appendix.

*General Times and Schedule effects.* The first GLM (GLM1) aimed to examine the general effects of Times and Schedule on episodic retrieval for both original and modified episodes. We included nine regressors for video trials, one per factorial combination of version$_{\text{FMRI}}$ (*ori*, *mod*), Times (*2*, *8*) and Schedule (*spaced*, *massed*), and one for novel videos. Please note, each factor level of the factors Times and Schedule contained two original and four modified videos. All video trials were modeled as epochs with onsets time-locked to the beginning of the videos and containing the full video duration. In addition, we included two regressors for the 18 null events and the 56 question trials. Null events were modeled as epochs, questions were modeled as events. For GLM1, we calculated the first-level-*t*-contrasts $8 > 2$ and $2 > 8$ to investigate the effect of Times. For the analysis of Schedule effects, we built the contrasts *spaced* > *massed* and *massed* > *spaced*.

*Phasic Times and Schedule effects at timepoint of modification.* With the second GLM (GLM2) we investigated the phasic effect of the expectancy violation at the precise moment it occurred. Regressors were the same as in GLM1, but video trials were modeled as events and onsets were time-locked to the point in the video at which the modification occurred. For the original videos, the onset used in each case was the time that corresponded, on average, to the onset of the structural and content change in the modified videos. For novel videos, the onset was set to the middle of the video. For GLM2, we calculated the contrasts $8 > 2$, $2 > 8$, *spaced* > *massed*, and *massed* > *spaced*. In addition, we calculated these contrasts separately for modified and unmodified episodes, that is, $mod_2 > mod_8$ and $mod_8 > mod_2$ as well as $mod_{spaced} > mod_{massed}$ and $mod_{massed} > mod_{spaced}$, and accordingly for originals. To investigate how Schedule and Times influence BOLD responses to mnemonic prediction errors, we built the interaction contrasts $(mod_2 > ori_2) > (mod_8 > ori_8)$, $(mod_8 > ori_8) > (mod_2 > ori_2)$, $(mod_{spaced} > ori_{spaced}) > (mod_{massed} > ori_{massed})$ and $(mod_{massed} > ori_{massed}) > (mod_{spaced} > ori_{spaced})$. As a control, we calculated another model in which the onsets for original videos corresponded to the times at which a modification would occur. The whole brain as well as ROI analyses yielded the same results as GLM2.

*Neuronal effects of later false alarm and correct rejections.* We used a third GLM (GLM3) to conduct an analysis that modeled BOLD responses according to the behavioral performance from the post-fMRI memory test to investigate which brain activity predicted later false memories, that is, false alarms in the memory test. GLM3 included regressors for null events (epochs), questions, original videos, and novel videos (events). Modified video trials were split into two separate regressors: those that were later (in the memory test) erroneously accepted as originals (false alarms [*fa*], originally Ratings 1 and 2) and those that were later correctly rejected (correct rejections [*cr*], originally Ratings 3 and 4). Please note that *fa* and *cr* for those episodes that had been presented in the modified version only in the post-fMRI memory test but not during scanning were not considered. Moreover, we added three further parametric modulators to model the repeated presentation of each video for original videos, modified videos resulting in *fa*, and modified videos resulting in *cr*. Six participants who did not have at least three false alarms (*fa*) or correct rejections (*cr*) in the memory test were excluded from this particular analysis. On average, there were 7.833 *fa* trials (*SD* = 2.730 trials) and 8.167 *cr* trials (*SD* = 2.730 trials) per participant.

*Effect of* TIMES *on neuronal response to later false alarms.* Finally, to investigate whether learning from prediction errors modeled by GLM3 depended on the employed retrieval protocol, we set up a fourth design, GLM4. As only TIMES yielded effects on memory performance, we focused on this factor and split the *fa* regressor into videos, which had been seen *2* times and videos that had been seen *8* times before participants entered the scanner ($fa_2$, $fa_8$). Following the same criterion as described above (minimally three later *fa* and three *cr* per regressor), this analysis included 22 participants. We calculated the contrasts for the parametric modulators from GLM3 and GLM4 to identify those brain regions in which the BOLD response increased with the number of presentations of videos that resulted in false memories.

### *Regions of Interest Analyses*

With regard to our hypotheses on specific brain regions involved in memory formation as well as the detection of mismatching information, we performed ROI analyses for each GLM as described below.

To further explore the effect of retrieval SCHEDULE and TIMES in episodic memory, we performed an ROI analysis based on GLM1. Anatomical ROIs were the bilateral HC and the bilateral FMC, according to our hypotheses. Based on the finding by Jainta et al. (2022), we restricted the FMC analysis to ACC, which was found to be activated during episodic recall in the current paradigm. Following our whole-brain analysis, we extracted mean contrast estimates (y) against the implicit baseline for the regressors *2*, *8*, *spaced*, and *massed*, and calculated paired-samples *t* tests (two-tailed) in each region. Next, we investigated whether the different retrieval protocols influenced neuronal processing of mnemonic prediction errors with a ROI analysis based on GLM2. ROIs were the bilateral HC (anatomical ROI) and regions we previously found to respond to mnemonic prediction errors, bilateral superior parietal lobe (SPL) and bilateral inferior frontal sulcus (IFS) (functional ROIs; data from Jainta et al., 2022). Contrast estimates for separate *mod* > *ori* contrasts, allocated to the factors SCHEDULE (*spaced*, *massed*) and TIMES (*2*, *8*), were extracted and rmANOVAs with the same factors were computed (nonparametric for hippocampal ROI as prerequisites for parametric analysis were not met). In addition, we conducted a ROI analysis for GLM3 to investigate the increasing parametric response to later false memories (i.e., gradual memory formation). Anatomical ROIs were the HC and the parahippocampal gyrus (PHG), both highly involved in learning (Davachi & Wagner, 2002; Köhler, Crane, & Milner, 2002; O'Reilly & Rudy, 2000; Aguirre, Detre, Alsop, & D'Esposito, 1996). Contrast estimates extracted from the three parametric modulators for *fa*, *cr*, and *ori* were first subjected to one-sample *t* tests (PHG) or one-sample Wilcoxon tests (HC) to analyze whether there was significant activity increase/decrease in these areas (one-tailed for *cr* and *fa*, two-sided for *ori*). Then, contrast estimates were compared with a rmANOVA (nonparametric for hippocampal ROI) and post hoc pairwise comparisons were conducted using paired *t* tests (one-tailed with respect to our hypotheses). We used the same ROIs to extract contrast estimates from GLM4. Here, we compared contrast estimates between the parametric modulators of $fa_2$ and $fa_8$ (paired *t* test, two-tailed). We report means and standard errors.

All anatomical ROIs were created using the automated anatomical labeling atlas (Tzourio-Mazoyer et al., 2002) from the Wake Forest University Pickatlas toolbox (Maldjian, Laurienti, Kraft, & Burdette, 2003) in SPM12. To create functional ROIs, we used the peak voxel coordinates from our previous study (contrast *mod* > *ori*; IFS: $x = 45, y = 26, z = 20$; $x = -42, y = 17, z = 23$; SPL: $x = 33, y = -61, z = 44$; $x = -30, y = -64, z = 41$) as the central points for spheres with a diameter of 6 mm. Mean contrast estimates were extracted using the MarsBar Toolbox (Brett, Anton, Valabregue, & Poline, 2002), aggregated over the left and right hemispheres.

## RESULTS

### Behavioral Results from Pre-fMRI Retrieval Sessions

To analyze the participants' performance during the pre-fMRI retrieval sessions, we calculated the correct answer rate for each combination of the two factors SCHEDULE and TIMES and performed a nonparametric rmANOVA. We found a significant main effect of TIMES, $F(1, 35)$ =

190.39, $p < .001$, $\eta_p^2 = .84$, as participants gave more correct answers when they retrieved the episode 8 instead of 2 times ($M_8 = .897 \pm .008$, $M_2 = .667 \pm .022$). There was a trend toward higher correct answer rates in the massed condition ($M_{\text{massed}} = .805 \pm .013$, $M_{\text{spaced}} = .758 \pm .020$), but the difference was not significant, $F(1, 35) = 3.13$, $p = .09$, $\eta_p^2 = .08$. There was no significant interaction, $F(1, 35) = 1.19$, $p = .28$, $\eta_p^2 = .03$.

### Behavioral Results from the Cover Task during fMRI

To ensure that participants paid attention during the scanning phase, they occasionally (after 33.33% of the videos) had to answer questions about the content of the video. A nonparametric rmANOVA on error rates during the fMRI experiment with the factor stimulus retrieval Times (*8*, *2*), Schedule (*spaced*, *massed*), and fMRI modification mode Modification$_{\text{FMRI}}$ (*yes*, *no*) revealed a trend for an interaction of Modification$_{\text{FMRI}}$ and Schedule, $F(1, 35) = 2.95$, $p = .095$, $\eta_p^2 = .078$. Descriptively, error rates were higher for original episodes, which had been retrieved in a spaced compared with a massed fashion. This difference could not be observed for modified videos ($M_{\text{no-spaced}} = .045 \pm .012$; $M_{\text{no-massed}} = .010 \pm .006$; $M_{\text{yes-spaced}} = .031 \pm .006$; $M_{\text{yes-massed}} = .033 \pm .008$). Participants generally made only few mistakes, with error rates of .028 ± .007 (mean ± standard error of mean) for unmodified videos and .032 ± .005 for modified videos. The error rate for the control condition (novel videos) was .073 ± .014.

Regarding RTs on correct trials, we found a significant main effect of Modification$_{\text{FMRI}}$, $F(1, 35) = 5.70$, $p = .022$, $\eta_p^2 = .140$, indicating that participants correctly recognized the story content of a video faster when presented with an unmodified version ($M_{\text{no}} = 951.653 \pm 26.821$ msec) compared with videos containing a modification ($M_{\text{yes}} = 973.455 \pm 27.912$ msec), although modification was task-irrelevant. Furthermore, we found a trend that RTs were longer for actions trained in a spaced ($M_{\text{spaced}} = 970.808 \pm 27.584$ msec) compared with a massed fashion ($M_{\text{massed}} = 954.300 \pm 26.939$ msec), $F(1, 35) = 3.49$, $p = .070$, $\eta_p^2 = .091$. There were no significant interactions, but we found a trend for an interaction of Schedule and Times, $F(1, 35) = 2.94$, $p = .095$, $\eta_p^2 = .078$.

### Behavioral Results from the Post-fMRI Memory Test

To investigate the effects of different retrieval protocols on learning from prediction errors, we averaged rating scores and RTs to modified$_{\text{MT}}$ and unmodified$_{\text{MT}}$ videos separately for each factorial combination. Memory performance for modified$_{\text{MT}}$ videos reflects how successfully participants rejected modified videos as not matching the originally experienced episodes. In contrast, memory performance for unmodified$_{\text{MT}}$ videos reflects how successfully participants accepted unmodified videos as truly matching the originally experienced episodes. For both, successful rejection and successful detection, we examined how they were modulated by the factors Times and Schedule during retrieval.

#### *Rejection and RTs for Modified Videos*

We found a significant main effect of Modification$_{\text{FMRI}}$ on rating scores, $F(1, 35) = 12.45$, $p = .001$, $\eta_p^2 = .262$, showing reduced rejection for modified videos already presented in a modified version during fMRI ($M_{\text{yes}} = 2.429 \pm 0.103$ vs. $M_{\text{no}} = 2.125 \pm 0.100$). Moreover, there was a significant main effect of Times, $F(1, 35) = 10.37$, $p = .003$, $\eta_p^2 = .229$, suggesting that successful rejection of a modified version was reduced when the original version had been presented less often during the pre-fMRI retrieval sessions ($M_8 = 2.177 \pm 0.102$; $M_2 = 2.377 \pm 0.091$). There were no significant interaction effects (Figure 5A).

Thus, episodic prediction errors during fMRI may have resulted in additional encoding of these particular stories (i.e., learning of modified episodes), but to a greater extent for less frequently retrieved memories, whereas spaced or massed retrieval protocols had no effect. Therefore, participants' judgments on previously encoded memories were influenced by these additional memory traces and correct responses on old memories were more difficult to make.

This was also reflected in RTs. Here, participants took significantly longer to rate modified videos already presented in a modified version during fMRI ($M_{\text{no}} = 588.038 \pm 61.449$ msec; $M_{\text{yes}} = 695.545 \pm 96.154$ msec; $F(1, 22) = 4.63$, $p = .043$, $\eta_p^2 = .174$). There were neither significant interaction effects nor further main effects (Figure 5B).

#### *Acceptance and RTs for Unmodified Videos*

We found a significant main effect of Modification$_{\text{FMRI}}$, $F(1, 35) = 40.03$, $p < .001$, $\eta_p^2 = .534$, indicating that participants were more likely to accept unmodified versions as originally encoded when already presented in their original form during fMRI ($M_{\text{no}} = 3.858 \pm 0.043$; $M_{\text{yes}} = 3.753 \pm 0.039$). We further found a significant main effect of Times, $F(1, 35) = 5.49$, $p = .025$, $\eta_p^2 = .136$, reflecting higher acceptance for more frequently retrieved episodes ($M_8 = 3.825 \pm 0.029$ vs. $M_2 = 3.786 \pm 0.048$). The interaction between Schedule and Times was also significant, $F(1, 35) = 10.12$, $p = .003$, $\eta_p^2 = .224$). Post hoc analyses with Wilcoxon pairwise tests (one-tailed) did not reveal significant differences between the levels of the factors Schedule and Times (*massed-2* vs. *massed-8*: $Z = -0.87$, $p = 1$; *massed-8* vs. *spaced-8*: $Z = -1.48$, $p = .552$; *spaced-2* vs. *spaced-8*: $Z = -1.06$, $p = 1$; *massed-2* vs. *spaced-2*: $Z = -1.26$, $p = .824$). However, when

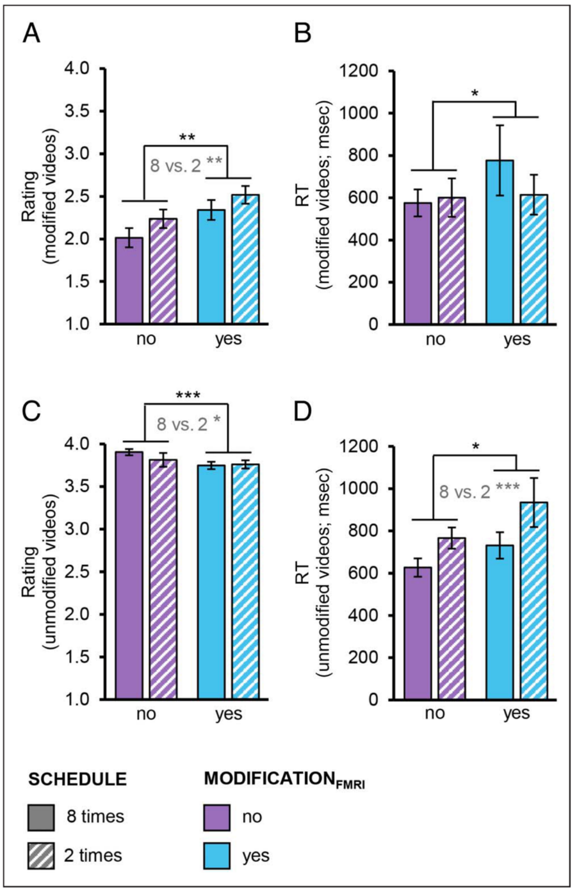

**Figure 5.** Behavioral results from post-fMRI memory test. Episodes had either been retrieved 8 or 2 times (factor Times) following a spaced or massed schedule (factor Schedule) before entering the fMRI session during which episodes were shown in an original or modified version (factor Modification$_{\text{FMRI}}$). Higher ratings reflect higher acceptance. (A) Ratings for modified videos. Statistics: nonparametric rmANOVA based on aligned rank data. (B) RTs for modified videos. Statistics: rmANOVA. (C) Ratings for unmodified videos. Statistics: nonparametric rmANOVA based on aligned rank data. (D) RTs for unmodified videos. Statistics: rmANOVA. *$p < .05$, **$p < .01$, ***$p < .001$. For more clarity, the factor Schedule is not depicted here. For a graph covering all factors, please see Appendix A (Figure A1).

retrieval had been scheduled in a massed fashion, participants were descriptively more likely to correctly recognize an unmodified episode after retrieving it 8 times ($M_{massed\text{-}8}$ = 3.795 ± 0.042) versus twice ($M_{massed\text{-}2}$ = 3.764 ± 0.062), and this pattern was even more pronounced in absolute values for the spaced condition ($M_{spaced\text{-}8}$ = 3.854 ± 0.031; $M_{spaced\text{-}2}$ = 3.809 ± 0.054). That is, the factor Times descriptively had an overadditive effect on the spaced Schedule. Finally, there was a significant three-way interaction of Modification$_{\text{FMRI}}$, Schedule, and Times, $F(1, 35) = 7.37, p = .01, \eta_p^2 = .174$ (Figure 5C). Accordingly, repeated triggering of the original episode led to better recall performance, especially if it had been retrieved more frequently before. Please note, however, that acceptance ratings in all conditions were at ceiling level (Figure 5C).

In line with the ratings, RTs to unmodified videos were faster when presented in their original version during fMRI ($M_{\text{no}}$ = 696.243 ± 38.372 msec; $M_{\text{yes}}$ = 832.948 ± 81.726 msec), $F(1, 34) = 7.14, p = .012, \eta_p^2 = .173$. In addition, a significant main effect of Times, $F(1, 34) = 13.63, p < .001, \eta_p^2 = .286$, indicated faster responses for more frequently retrieved episodes ($M_8$ = 679.031 ± 44.506 msec, $M_2$ = 850.160 ± 74.799 msec; Figure 5D).

### *Ratings for Novel Videos*

Participants were clearly aware that novel videos had not been part of the originally encoded episodes, as indicated by floor-level rating scores (i.e., successful rejections; rating: $M$ = 1.021 ± 0.015) and very fast RTs ($M$ = 624.316 ± 55.878 msec).

## fMRI Results

### *Neural Effects of Different Retrieval Protocols*

To analyze the influence of the factor Times on brain activation during re-exposure to episodes (GLM1), we calculated whole-brain contrasts *8 > 2* and *2 > 8*. For both contrasts, we did not detect significant increases in brain activity.

Following our hypotheses, we performed ROI analyses to investigate how retrieval Times influence brain activation. Based on a previous study (Jainta et al., 2022), we used anatomical ROIs of the bilateral ACC and the bilateral HC and calculated paired-samples $t$ tests (two-tailed) for each brain region to compare conditions. Contrast estimates were extracted from conditions for 2 and 8 (contrasted against the implicit baseline) using GLM1. We did not find a significant effect of retrieval Times. Descriptively, contrast estimates in ACC were lower for 8 versus 2 times, $t(35) = 0.93, p = .36, d = .155$; $M_2 = -0.811 \pm 0.128$, $M_8 = -0.872 \pm 0.121$. This descriptive pattern was also present in the HC, $t(35) = 1.18, p = .25, d = .196$; $M_2 = -0.116 \pm 0.044$, $M_8 = -0.137 \pm 0.044$.

Based on our hypothesis that spacing practice of retrieval between encoding and fMRI sessions will lead to more stable memory trace, we investigated how spaced versus massed Schedule during retrieval influence neural activation for episodes in general. Here, we calculated the whole-brain contrasts *spaced > massed* and *massed > spaced*. For the contrast *spaced > massed*, we found increased activity in the bilateral posterior cingulate cortex (pCC), the bilateral SPL/ intraparietal sulcus (IPS), and the right posterior precuneus (PCUN; Table 1, Figure 6) whereas we did not find significantly greater activity for the contrast *massed > spaced*.

Following our hypotheses that retrieval Schedule influences brain activation, we again performed ROI analyses and extracted contrast estimates from spaced and massed

**Table 1.** Peak Activations from Second-level Whole-brain Analyses of Retrieval Schedule

| | | | *MNI Coordinates* | | | |
|---|---|---|---|---|---|---|
| *Localization* | *H* | *Cluster Extent* | *x* | *y* | *z* | *t Value* |
| *spaced > massed (FDR-corrected at p < .05)* | | | | | | |
| Superior parietal lobe/intraparietal sulcus | R | 25 | 27 | −67 | 59 | 5.27 |
| | L | 66 | −30 | −64 | 56 | 4.95 |
| Posterior PCUN | R | 44 | 12 | −61 | 32 | 4.24 |
| Posterior cingulate cortex | R | 60 | 6 | −37 | 29 | 5.59 |
| | L | l.m. | −6 | −34 | 32 | 5.15 |

H = Hemisphere; MNI = Montreal Neurological Institute; L = Left; R = Right; l.m. = local maximum.

conditions (GLM1). We found a near-significant trend of retrieval Schedule on brain activity for episodes in HC, as contrast estimates were higher for spaced compared with massed retrieval, $t(35) = 1.90$, $p = .066$, $d = .316$; $M_{\text{spaced}} = -0.111 \pm 0.042$, $M_{\text{massed}} = -0.142 \pm 0.046$. This was not the case in ACC, $t(35) = 0.02$, $p = .99$, $d = .003$; $M_{\text{spaced}} = -0.84 \pm 0.128$, $M_{\text{massed}} = -0.842 \pm 0.120$.

### *Effects of Retrieval Protocols on Neural Responses to Modified Cueing*

In our previous analysis of this data set, we demonstrated that several brain regions respond to mnemonic prediction errors (*mod* > *ori*; Siestrup et al., 2022). To now understand the influence of previous retrieval Times on brain activation for modified episodes, we calculated the contrasts $mod_2 > mod_8$ and $mod_8 > mod_2$ (GLM2). Regarding the $mod_2 > mod_8$ contrast, we found increased activity in ACC (Brodmann's area [BA] 24 and BA 32; Table 2, Figure 6B). The contrasts *2* > *8* as well as $ori_2 > ori_8$ did not yield significant results, indicating that this effect might be specific for modified videos. The reverse contrast, $mod_8 > mod_2$, did not result in significant effects. For further (subthreshold) results from GLM2, please see Appendix B. Furthermore, we analyzed interaction effects of retrieval protocols, which are reported in Appendix C.

To further elucidate the impact of different retrieval protocol on neural responses for mnemonic prediction errors, we conducted ROI analyses by extracting contrast estimates from GLM2 for separate *mod* > *ori* contrasts, allocated to the factors Schedule (*spaced*, *massed*) and Times (*2*, *8*). These yielded no significant results in IFS or SPL. In the hippocampal ROI, we found a significant main effect of Schedule, $F(1, 35) = 4.86$, $p = .034$, $\eta_p^2 = .122$, driven by higher contrast estimates for massed than for spaced ($M_{\text{massed}} = 0.035 \pm 0.051$, $M_{\text{spaced}} = -0.151 \pm 0.050$). There was no main effect of Times, $F(1, 35) = 0.05$, $p = .829$, $\eta_p^2 = .001$, and no significant interaction, $F(1, 35) = 0.04$, $p = .85$, $\eta_p^2 = .001$.

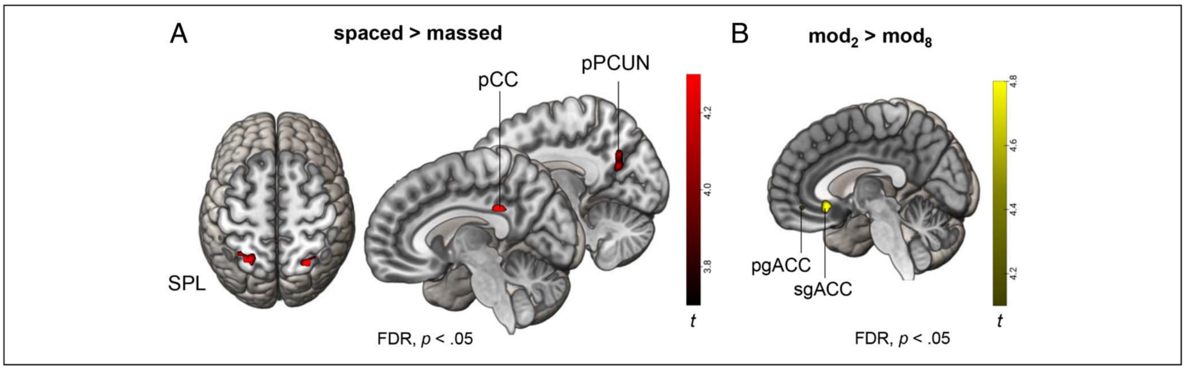

**Figure 6.** Whole-brain activation for retrieval Schedule and Times effects. (A) FDR-corrected *t*-map ($p < .05$) for the *spaced* > *massed* contrast in episodes (based on GLM 1). (B) FDR-corrected *t*-map ($p < .05$) for the $mod_2 > mod_8$ contrast (based on GLM 2). pCC = posterior cingulate cortex; SPL = superior parietal lobe; pPCUN = posterior precuneus; pgACC = pregenual anterior cingulate cortex; sgACC = subgenual anterior cingulate cortex.

**Table 2.** Peak Activations from Second-level Whole-brain Analyses of Retrieval Times for Modified Episodes

| | | | *MNI Coordinates* | | | |
|---|---|---|---|---|---|---|
| *Localization* | *H* | *Cluster Extent* | *x* | *y* | *z* | *t Value* |
| *$mod_2 > mod_8$ (FDR-corrected at $p < .05$)* | | | | | | |
| Subgenual ACC (BA 24) | R | 13 | 3 | 23 | −13 | 6.04 |
| Pregenual ACC (BA 32) | L + R | 7 | 0 | 44 | −13 | 5.09 |

H = Hemisphere; MNI = Montreal Neurological Institute; L = Left; R = Right; BA = Brodmann's area.

### *Parametric Effects of Episode Repetition for Later False Alarms*

We were interested in how behavioral performance was reflected in brain activity during repeated reactivation of episodes. To investigate the neural effects of memory modification, we analyzed the parametric increase in brain activation to modified episodes that later elicited false memories (GLM3). The BOLD response increased with repeated presentation of a modified episode, when it was later misclassified as original, in several regions: superior frontal gyrus (SFG) extending into ACC, as well as in inferior frontal gyrus, IPS, midcingulate cortex, pCC, and middle temporal cortex (Table 3, Figure 7A).

**Table 3.** Peak Activations from Second-level Whole-brain Analyses of Parametric Effect (Increase) for Later False Memories

| | | | *MNI Coordinates* | | | |
|---|---|---|---|---|---|---|
| *Localization* | *H* | *Cluster Extent* | *x* | *y* | *z* | *t Value* |
| *Parametric modulator (fa; FDR-corrected at $p < .01$)* | | | | | | |
| Superior frontal gyrus e.i. ACC (lateral BA 9 e.i. BA 10) | L | 550 | −9 | 38 | 50 | 5.48 |
| Middle frontal gyrus | L | l.m. | −33 | 23 | 47 | 5.12 |
| Superior frontal gyrus | R | 6 | 6 | 38 | 56 | 4.39 |
| Middle frontal gyrus | R | 7 | 33 | 35 | 44 | 4.15 |
| Angular gyrus/inferior parietal sulcus | R | 37 | 57 | −46 | 44 | 4.35 |
| Angular gyrus | R | l.m. | 48 | −55 | 38 | 3.94 |
| PCUN | R | 7 | −12 | −43 | 41 | 4.01 |
| Angular gyrus | L | 124 | −51 | −61 | 38 | 5.30 |
| Supramarginal gyrus | L | l.m. | −51 | −52 | 29 | 4.89 |
| Midcingulate cortex | L | 57 | −6 | −16 | 32 | 4.89 |
| | R | l.m. | 3 | −19 | 35 | 4.41 |
| Posterior cingulate cortex | L | 21 | −3 | −43 | 26 | 4.58 |
| Superior temporal gyrus | R | 9 | −63 | −22 | 14 | 4.10 |
| Inferior frontal gyrus (pars triangularis) | L | 44 | −54 | 29 | 11 | 4.75 |
| Inferior frontal gyrus (pars orbitalis) | L | l.m. | −51 | 35 | −10 | 4.20 |
| Subgenual ACC | R | 12 | 3 | 20 | −4 | 4.65 |
| Middle temporal gyrus | L | 407 | −51 | −31 | −7 | 6.77 |
| | R | 322 | 57 | −22 | −10 | 7.33 |
| Inferior temporal gyrus | R | l.m. | 51 | −16 | −22 | 4.70 |
| Middle temporal pole | R | 16 | 48 | 14 | −28 | 5.14 |
| Cerebellum | L | 52 | −24 | −91 | −34 | 4.69 |
| | R | 233 | 30 | −85 | −40 | 5.54 |

H = Hemisphere; MNI = Montreal Neurological Institute; L = Left; R = Right; e.i. = extending into; l.m. = local maximum.

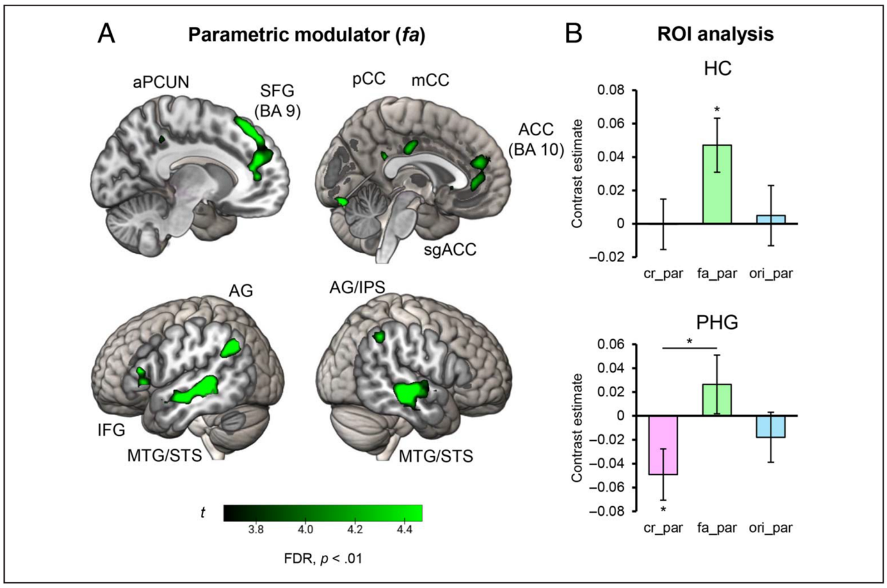

**Figure 7.** Results from the parametric analysis. (A) FDR-corrected $t$-map ($p < .01$) for the whole-brain contrast of the parametric modulator modeling the repeated presentation of modified episodes, which lead to false alarm responses in the post-fMRI memory test. Activation clusters indicate an increase of brain activity with repeated exposure. aPCUN = anterior precuneus; SFG = superior frontal gyrus; BA = Brodmann's area; pCC = posterior cingulate cortex; mCC = midcingulate cortex; sgACC = subgenual anterior cingulate cortex; AG = angular gyrus; IFG = inferior frontal gyrus; MTG = middle temporal gyrus; STS = superior temporal sulcus; IPS = intraparietal sulcus. (B) ROI analysis for parametric modulators modeling the repeated presentation of modified episodes, which were later false alarms (fa_par) or correct rejections (cr_par), as well as parametric response to original episodes (ori_par). Contrast estimates were extracted from hippocampal complex (HC) and parahippocampal gyrus (PHG). Statistics: one-sample $t$/Wilcoxon tests; rmANOVA (nonparametric for HC ROI) and paired $t$ tests (one-tailed). $^*p < .05$.

Following this whole-brain analysis, we performed a ROI analysis to specifically investigate brain responses in areas that are highly involved in memory formation, HC and PHG, as hypothesized. In HC, we found a significant increase of activation for *fa* ($Z = -2.92, p = .01$), whereas the change of activation was not significant for *cr* ($Z = -0.56, p = 1$), and *ori* ($Z = -0.18, p = 1$). In PHG, there was a significant decrease in activation for *cr*, $t(29) = -2.28$, $p = .04$, and no significant change of activation for *fa*, $t(29) = 1.07, p = .44$, and *ori*, $t(29) = -0.86, p = 1$. Using rmANOVA, we compared contrast estimates from the three parametric modulators for *fa*, *cr*, and *ori*. In HC, we found a trend for an effect of condition, $F(2, 58) = 3.0, p = .058$, $\eta_p^2 = .094$, as descriptively seen from an increase for false alarms versus a decrease for correct rejections (Figure 7B). In PHG, the same effect was significant, $F(2, 58) = 3.26, p = .045$, $\eta_p^2 = .101$. Paired $t$ tests showed that contrast estimates in PHG were significantly higher for the parametric *fa* than for the parametric *cr* response, $t(29) = -2.40$, $p = .034$, $d = -.439$, as expected (Figure 7B). The remaining pairwise comparisons did not yield significant results (cr_par vs. ori_par: $t(29) = -1.05, p = .45, d = -.193$; fa_par vs. ori_par: $t(29) = 1.58, p = .19, d = .289$).

Regarding effects of how the factor Times influenced learning from prediction errors (GLM 4), we performed ROI analysis on HC and PHG. As we only found subthreshold effects, we report the results in Appendix D.

## DISCUSSION

When we encounter a previously experienced episode, the brain reactivates a memory trace, corroborating its stability while also allowing flexible adaptations to cope with upcoming changes in the world (Lee et al., 2017). In this study, we took the view that retrieval, and modification of episodic memories upon retrieval, should be influenced by how strongly memories were consolidated. Specifically, we investigated the effects of different retrieval protocols, namely, the temporal schedule of retrieval practice (in the following referred to as retrieval schedule) and the amount of practice. To separately test stability induced by these two factors, we violated episodic expectations using subtly modified retrieval cues and assessed the effects of this prediction error on brain activity and subsequent memory performance.

### Evidence for Learning through Prediction Errors

Concerning the post-fMRI memory test, we replicated our previous finding that repeatedly experiencing modified episodes during the fMRI session leads to a higher misattribution of the same modified versions as part of the original episode repertoire (Jainta et al., 2022). Again, we saw that, following the presentation of the modified version in the scanner, original videos received less acceptive ratings. Still, there was a ceiling effect concerning ratings for original videos; as in all conditions, acceptance was extremely high. Our findings suggest that episodic prediction errors lead to the encoding of an alternative representation of the same episode, rather than replacing the original representation based on new information. What remains unclear is how exactly original memories were influenced by the acquisition of alternative (nonveridical) episodes. For example, memories might be modified through remodeling of the original memory trace, or through source confusion or interference effects. A detailed discussion of this aspect is provided in Siestrup et al. (2022).

A set of neocortical areas and the hippocampal formation showed a BOLD response that increased with repeated presentation of the same modified episode when this modified episode was later mistaken as originally experienced. This cerebral reflection of incremental learning because of repeated prediction errors was found in superior and inferior frontal areas, the cingulate cortex, as well as in the middle temporal and superior parietal cortex. Hypothesis-driven ROI analyses in the hippocampal formation revealed that, whereas activation to later correct rejections decreased with repeated encounters, activation to later false alarms increased, as expected. To our knowledge, this is the first demonstration of a specific and dynamic learning effect induced by episodic prediction errors.

Hippocampus and neocortical areas are suggested to be concurrently active during learning of new events, and encoded memories become more and more independent of hippocampal activity, which initially aids encoding by detailed but short-lived storage run (Frankland & Bontempi, 2005). Thus, the hippocampus was found to support the development of a neocortical memory representation during first stimulus encounters, but then decreased in activity during further encounters with the learned stimulus (Brodt et al., 2016). Notably, in Brodt and colleagues' work, learning was based on recurrent experience of unmodified object–location information without a particular necessity to update memory. Against this backdrop, our findings speak in favor of sustained learning in both neocortical and hippocampal areas when participants repeatedly encountered slightly modified episodic cues. In our paradigm, sustained hippocampal engagement during ongoing learning could be because of the fact that the repetitions of a modified episode did not occur consecutively, but in randomized sequences intermixed with other modified and original episodes. Another unique feature was that a preexisting memory trace was activated and involved in a learning process. This mixture of familiar and novel parts in the same stimulus placed particularly high demands on associative learning, resulting in participants accepting both the original and the modified episode as belonging to the originally learned set. Note that during the fMRI session, each participant was exposed only to either the modified or the original version of an episode.

For the interpretation of our findings, it was particularly informative that successful learning of the modified episode depended on the presence of sustained hippocampal activity. This could be concluded from the fact that modified episodes that were later correctly rejected as nonoriginal showed no such increase in hippocampal areas.

Our results suggest the formation of additional memory traces, specifically "alternative versions" of previously encoded episodes, which are later erroneously taken as veridically experienced, through engagement of the episodic memory network, including the HC, medial frontal cortex, posterior cingulate, lateral temporal areas, and temporo-parietal junction (Jeong, Chung, & Kim, 2015). In addition to these well-known components for episodic encoding and retrieval, there were two brain sites that do not typically show up for episodic processes: BA 9m and mid-cingulate cortex. We refrain from broadly discussing these findings post hoc but would like to suggest how they may contribute to modification processes of episodic information, awaiting to be tested in future studies. On the one hand, the mid-cingulate cortex has been suggested to contribute to the monitoring of the other's decisions (Apps, Lockwood, & Balsters, 2013). This functional description dovetails with the fact that our participants experienced a subtle breach of episodic expectation regarding a change in the videotaped toy story. Although they later judged this modified episode to be veridically self-experienced, the brain seemed to detect this specific prediction error as if witnessing an unexpected decision. On the other hand, BA 9 has been reported to be increasingly activated for the emergence of coherence between contextual relations (Ferstl, Neumann, Bogler, & von Cramon, 2008), for example, in the presentation of syntactically independent but episodically related sentences (Ferstl & von Cramon, 2001, 2002). Although these studies were very different from ours, the concept of coherence could be an interesting starting point for understanding the role of BA 9 in episodic modification: This area could detect and code coherence between similar episodic events, which in our study led to modified episodes being accepted as originals during post-fMRI memory testing.

### Effects of Pre-fMRI Retrieval Frequency

In line with our hypotheses, memory for originally encoded episodes was better when participants had retrieved episodes 8 times compared with 2 times before the fMRI session. This was evidenced by more rejective ratings for modified videos, slightly (but significantly) more acceptive ratings for unmodified videos and shorter RTs for the latter. This pattern already emerged during the pre-fMRI retrieval sessions, as episodes retrieved 8 times had an overall higher percentage of correct responses. Our findings contribute to the large body of literature reporting the same effect (Lyle et al., 2020; Karpicke & Roediger, 2007; Underwood, 1970). The benefit of eight previous repetitions was also present when modified episodes had been presented during the fMRI session, which is in line with reports that retrieval practice can protect memories from modification (Scully & Hupbach, 2020; Pastötter, Eberle, Aue, & Bäuml, 2017; Bäuml, Holterman, & Abel, 2014; Rowland, 2014; Potts & Shanks, 2012; Halamish & Bjork, 2011).

Interestingly, we did not find increased neural activation after more frequent retrievals (*8* vs. *2*) when investigating the general effects of retrieval protocols, as would be expected in areas where memory representation is established. On the contrary, when focusing on modifications in episodes, we found evidence for decreasing activation as one would associate it with decreasing effort of retrieval ($mod_8 < mod_2$); this effect was found for ACC, an area that was reported to decrease in activity with progressing consolidation (Long et al., 2016). In addition, we found that the brain response to mnemonic prediction errors was modulated by previous retrieval times in a similar fashion, as the interaction contrast ($mod_2 > ori_2$) > ($mod_8 > ori_8$) revealed subthreshold activation in ACC and FMC (BA 9 and 10). Hence, it seems that less stable memories might be more effortful to retrieve, which yields elevated brain activation in areas associated with episodic recall (Nadel et al., 2007). Schiffer and colleagues (2013) detected activity in ACC and medial frontopolar cortex (BA 10) when comparing the influence of prediction errors on biased versus balanced internal models, suggesting that the adaptation of internal models because of prediction errors occurred more slowly for strong and faster for weak internal models (Schiffer et al., 2013). As mentioned, the FMC is activated through the experience of prediction errors (Malekshahi et al., 2016; Schiffer et al., 2013). Regarding our findings, the FMC may indicate the level of coherence between previously encoded and currently perceived modified episodes, which further corroborates our interpretation of these areas being involved in model updating. We interpret activity in these areas to indicate the detection of mismatching information as well as the increasing familiarity with perceived modifications over time while comparing them to mnemonic representations. Accordingly, in the case of weaker mnemonic representations (hence, weaker predictive models), prediction errors potentially serve as a more potent signal for model updating (i.e., learning). These findings extend the general functional view of ACC as a region involved in conflict processing (Vassena, Holroyd, & Alexander, 2017; Botvinick, Cohen, & Carter, 2004) and learning from (prediction) errors to adapt behavior (Vassena et al., 2017; Rushworth, Noonan, Boorman, Walton, & Behrens, 2011).

It has previously been discussed that there is likely no linear relationship between the number of retrievals and later retention (Rowland, 2014; Roediger & Butler, 2011). Potentially, most mnemonic benefit is gained from increasing the retrieval frequency from one to two retrievals (Lyle et al., 2020; Rawson & Dunlosky, 2011). Therefore, it could be that several meaningful changes in neuronal activation arise at this threshold. In this study, the lowest retrieval frequency already exceeded this potential level of highest consolidation benefit, which might explain our partially subtle findings.

### Effects of Spaced versus Massed Retrieval Protocols

Our data did not confirm previous findings that spaced retrievals result in better memory for originally encoded episodes compared with massed retrievals (Latimier, Peyre, & Ramus, 2021; Lyle et al., 2020; YeckehZaare et al., 2019; Kang, 2016; Gerbier & Toppino, 2015; Dempster, 1989; Underwood, 1970). There is still an ongoing debate on how to design spaced practice schedules to maximize the positive influence on retention. While some suggest that spacing out practice to two sessions is already highly effective (Gerbier & Toppino, 2015), others report that the spacing effect is more powerful for a higher number of distributed sessions (Dobson et al., 2017). In addition, some researchers suggest that the first of multiple retrieval sessions should occur shortly after initial encoding, like in our paradigm, as this maximizes the likelihood of successful retrieval. However, others argue that this limits the benefit for long-term retention as the first retrieval might not be effortful enough (Kang, 2016; Roediger & Butler, 2011). Our paradigm followed the naturalistic timeline of first encoding an episode into memory and then retrieving it at different timepoints, which contributes to memory consolidation. Similar designs have been used previously in memory research when investigating the influence of massed versus spaced retrieval on retention (e.g., Lyle et al., 2020; Karpicke & Bauernschmidt, 2011; Landauer & Björk, 1978). However, practice might only be truly “massed” if carried out during a single encounter (e.g., Kang, 2016). Encountering episodes in the encoding as well as in the retrieval session might have decreased the differences between spaced and massed retrieval in the current work.

The fMRI analysis of general retrieval protocol effects revealed significant activation for episodes that had been retrieved following a spaced schedule in SPL/IPS, PCUN, and pCC, which are all involved in episodic remembering. Hippocampal involvement was slightly higher (trend) in the spaced condition, as revealed by the ROI analysis (Jainta et al., 2022; Sestieri, Shulman, & Corbetta, 2017; Rugg & Vilberg, 2013; Trimble & Cavanna, 2008; Cavanna & Trimble, 2006; Iidaka, Matsumoto, Nogawa, Yamamoto, & Sadato, 2006; Wagner, Shannon, Kahn, & Buckner, 2005). Interestingly, we found that for the processing of prediction errors, massed retrieval generally led to increased brain activation in comparison to spaced retrieval. The interaction analysis concerning the influence of retrieval schedule on the processing of mnemonic prediction errors ($mod_{massed} > ori_{massed}$) > ($mod_{spaced} > ori_{spaced}$) yielded subthreshold activation in pre- and postcentral gyrus as well as in the superior temporal gyrus. The ROI analysis revealed higher hippocampal engagement in the processing of prediction errors in the massed condition. However, because of the lack of a behavioral effect, it is difficult to interpret these findings in terms of memory stability. Descriptively increased error rates and RTs during the fMRI task for episodes from the spaced condition might indicate that they were more difficult to retrieve, that is, less consolidated. Notably, this interpretation is speculative, because the fMRI task was designed to ensure constant attention and not to probe memory. However, together with the lack of behavioral effects, it opens the possibility that our spaced versus massed retrieval schedule was not yet quantitatively sufficient to benefit from spaced retrieval and to produce behavioral effects. As outlined above, more research is needed to identify an optimal spacing strategy. We believe that repeating our study with an updated spacing schedule will benefit the understanding of its influence on memory consolidation on a neuronal level.

### Limitations

In this study, we found effects of retrieval schedule and retrieval times for modified, but not original, videos. When interpreting the results of this study, we must acknowledge that the statistical power of modified videos compared with originals may be stronger because of an unbalanced number of trials within the two conditions. Participants were presented with twice as many modified videos (16) compared with originals (eight) during fMRI. We cannot rule out the possibility that null-results in original videos may result from a lower number of videos per condition. However, we showed in a previous analysis that subdividing modified videos into two different types of expectation violation including eight videos per condition still led to substantial brain responses (Siestrup et al., 2022). Compared with original videos, both violation types shared activity patterns in frontal and parietal areas. Although these previous results increase the reliability of our present results, further research is still needed.

Furthermore, alternative explanations for our behavioral findings can be considered. On the one hand, it is possible that modified episodes presented during the fMRI session were later endorsed as originals because of the additional recent encoding opportunity. In this respect, it is worth noting that novel videos, which were also repeatedly encountered during the fMRI session, were not mistaken for original episodes by the participants. Therefore, it is unlikely that recency drove the observed effects. On the other hand, it is possible that participants mistook modified episodes as original ones after several repetitions during the fMRI session because of increased familiarity with these episodes. However, familiarity alone would not account for the clear distinction of neuronal responses to later false alarms and correct rejections, as all modified videos were equally familiar. Nevertheless, further research is needed to understand the direct contribution of prediction errors to memory modification.

### Conclusion

Episodic memories can change upon retrieval, and episodic prediction errors may trigger this process. In this study, we found that episodic prediction errors led to a dynamic learning process in the episodic memory network, resulting in the acceptance of false memories as veridical. Moreover, different retrieval protocols modulated the brain responses to episodic prediction errors and changed the subsequent propensity to learn from these events. These observations may be a fruitful starting point for further investigation of episodic prediction errors and their role in episodic memory changes.

## APPENDIX A

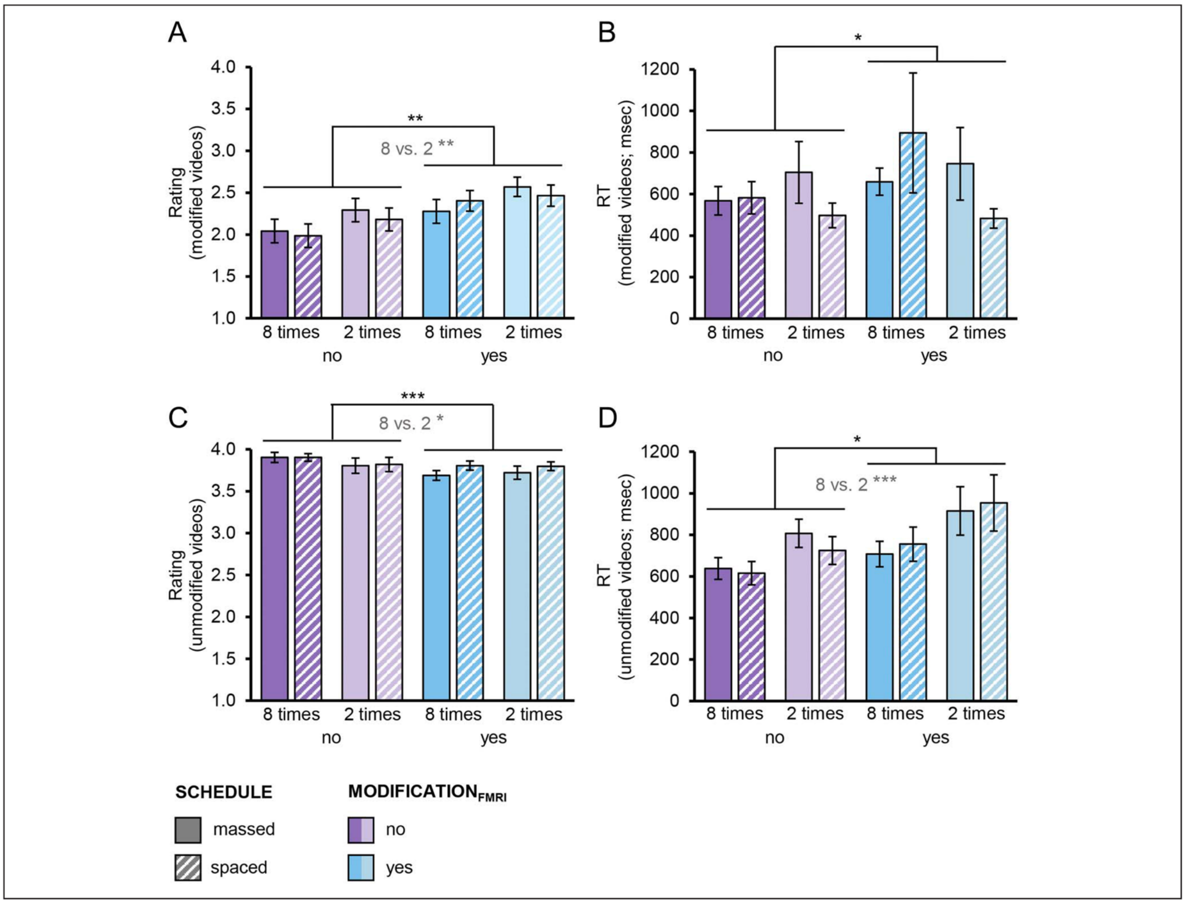

**Figure A1.** Behavioral results from post-fMRI memory test for all factors. Episodes had either been retrieved 8 or 2 times (factor Times) following a spaced or massed schedule (factor Schedule) before entering the fMRI session during which episodes were shown in an original or modified version (factor Modification$_{\text{FMRI}}$). Higher ratings reflect higher acceptance. (A) Ratings for modified videos. Statistics: nonparametric rmANOVA based on aligned rank data. (B) RTs for modified videos. Statistics: rmANOVA. (C) Ratings for unmodified videos. Statistics: nonparametric rmANOVA based on aligned rank data. (D) RTs for unmodified videos. Statistics: rmANOVA. *$p < .05$, **$p < .01$, ***$p < .001$.

## APPENDIX B

To investigate the effects of previous retrieval Schedule on brain activation for modified episodes, we calculated the contrasts $mod_{spaced} > mod_{massed}$ and $mod_{massed} > mod_{spaced}$ (GLM2). Both contrasts did not reveal significant activation with FDR correction. However, for $mod_{massed} > mod_{spaced}$, we found subthreshold activation in cerebellum (right hemisphere: 23 voxels, $x = 42, y = -46, z = -31$; left hemisphere: 24 voxels, $x = -18, y = -61, z = -43$). No contrast for original episodes yielded significant results. Subthreshold activation for $ori_8 > ori_2$ was found in the right superior frontal sulcus and insula, as well as in the left middle frontal gyrus. For $ori_{spaced} > ori_{massed}$, we detected subthreshold activation in the left central sulcus and in the superior temporal sulcus (Table B1).

**Table B1.** Peak Activations from Second-level Whole-brain Analyses of Retrieval Times and Schedule for Original Episodes

| | | | *MNI Coordinates* | | | |
|---|---|---|---|---|---|---|
| *Localization* | *H* | *Cluster Extent* | *x* | *y* | *z* | *t Value* |
| *$ori_8 > ori_2$ (uncorrected at $p < .001$)* | | | | | | |
| Superior frontal gyrus | R | 19 | 21 | 59 | 23 | 3.83 |
| Middle frontal gyrus | L | 10 | −39 | 53 | 17 | 3.77 |
| Insula | R | 11 | 39 | 14 | −16 | 4.43 |
| *$ori_{spaced} > ori_{massed}$ (uncorrected at $p < .001$)* | | | | | | |
| Sulcus centralis | L | 76 | −57 | −16 | 47 | 4.70 |
| Temporal pole (superior temporal gyrus) | L | 40 | −42 | 5 | −22 | 5.15 |

H = Hemisphere; MNI = Montreal Neurological Institute; L = Left; R = Right.

## APPENDIX C

To further understand the influence of previous retrieval Times and Schedule while controlling for potential baseline effects (GLM2), we analyzed interaction effects of retrieval protocols for mnemonic prediction errors. First, we investigated the influence of retrieval times on modified episodes in comparison to original episodes. The $(mod_2 > ori_2) > (mod_8 > ori_8)$ contrast revealed subthreshold activity in the left middle frontal gyrus (MFG; BA 9 and BA 10), bilateral SFG, right angular gyrus (AG), and left pregenual ACC (Table C1). Contrasting $(mod_{massed} > ori_{massed}) > (mod_{spaced} > ori_{spaced})$, we found a subthreshold activity in the bilateral postcentral gyrus, left superior temporal gyrus, and left amygdala (Table C1).

**Table C1.** Peak Activations from Second-level Whole-brain Analyses of Interaction Effects

| | | | *MNI Coordinates* | | | |
|---|---|---|---|---|---|---|
| *Localization* | *H* | *Cluster Extent* | *x* | *y* | *z* | *t Value* |
| *$(mod_2 > ori_2) > (mod_8 > ori_8)$ (uncorrected at $p < .001$)* | | | | | | |
| Angular gyrus | R | 27 | 60 | −55 | 32 | 4.49 |
| Superior frontal gyrus | L | 23 | −18 | 53 | 29 | 4.01 |
| | R | 40 | 18 | 59 | 20 | 4.66 |
| Medial superior frontal gyrus/mesial frontal cortex (BA 9) | L | 78 | −6 | 59 | 20 | 4.44 |
| Middle frontal gyrus | L | 8 | −36 | 50 | 17 | 3.65 |
| Caudate nucleus | R | 4 | 6 | 14 | 8 | 4.21 |
| ACC | R | 8 | 6 | 26 | −7 | 3.55 |
| Pregenual ACC/straight gyrus | L | 53 | −3 | 47 | −19 | 4.45 |
| Right insula | R | 7 | 36 | 14 | −19 | 3.80 |
| *$(mod_{massed} > ori_{massed}) > (mod_{spaced} > ori_{spaced})$ (uncorrected at $p < .001$)* | | | | | | |
| Postcentral gyrus | L | 165 | −48 | −22 | 56 | 4.69 |
| | R | 22 | 48 | −13 | 32 | 4.16 |
| Superior temporal gyrus | R | 9 | 66 | −10 | 5 | 3.87 |
| Hippocampus | R | 8 | 21 | −7 | −16 | 4.35 |
| Superior temporal gyrus | L | 40 | −39 | 8 | −22 | 4.54 |
| Amygdala | L | l.m. | −30 | 2 | −16 | 4.00 |

H = Hemisphere; MNI = Montreal Neurological Institute; L = Left; R = Right; BA = Brodmann's area; l.m. = local maximum.

## APPENDIX D

With regard to GLM4, we were interested whether learning from prediction errors during scanning predicted later false memories during the memory test. To investigate whether BOLD responses were influenced by the former retrieval protocol, we reanalyzed the behavioral performance during the post-fMRI memory test. As Times, but not Schedule, affected the stability of episodic memories as indicated by better recall, we tested whether different retrieval Times were reflected in brain areas involved during memory formation. Based on model GLM4, we extracted contrast estimates for parametric *fa* responses separately for episodes that had been retrieved 2 and 8 times. As a result, we found that the increasing BOLD effect did not depend on previous retrieval times in HC, $t(21) = -1.22$, $p = .23$, $d = -.261$; $M_{\text{fa2\_par}} = 0.014 \pm 0.020$, $M_{\text{fa8\_par}} = 0.072 \pm 0.039$, or PHG, $t(21) = -0.82$, $p = .42$, $d = -.176$; $M_{\text{fa2\_par}} = 0.014 \pm 0.029$, $M_{\text{fa8\_par}} = 0.056 \pm 0.048$.

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Reprint requests should be sent to Sophie Siestrup, Department of Psychology, University of Münster, Fliednerstraße 21, 48149 Münster, Germany, or via e-mail: s.siestrup@uni-muenster.de.

### Data Availability Statement

The data sets generated for this study are available on request to the corresponding author.

### Author Contributions

Sophie Siestrup: Formal analysis; Investigation; Methodology; Visualization; Writing—Original draft; Writing—Review & editing. Benjamin Jainta: Formal analysis; Investigation; Methodology; Visualization; Writing—Original draft; Writing—Review & editing. Sen Cheng: Conceptualization; Writing—Review & editing. Ricarda I. Schubotz: Conceptualization; Funding acquisition; Methodology; Resources; Supervision; Writing—Original draft; Writing—Review & editing.

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### Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

### Ethics Statements

The study was conducted in accordance with the Declaration of Helsinki and approved by the Local Ethics Committee of the University of Münster. Participants signed an informed consent before participation.

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## 3.3 Study 3: Same same, but different: Brain areas underlying the learning from repetitive episodic prediction errors

Running title: Effects of Repetitive Prediction Errors

Benjamin Jainta, Anoushiravan Zahedi & Ricarda I. Schubotz (2023)

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# Same same, but different: Brain areas underlying the learning from repetitive episodic prediction errors

**Benjamin Jainta[1, *], Anoushiravan Zahedi[1, 2], Ricarda I. Schubotz[1, 2]**

[1] Department of Psychology, University of Münster, Münster, Germany

[2] Otto Creutzfeldt Center for Cognitive and Behavioral Neuroscience, University of Münster, Münster, Germany

*** Correspondence:**
Benjamin Jainta
bjainta@uni-muenster.de

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## ABSTRACT

Prediction errors (PEs) function as learning signals. It is yet unclear, how varying compared to repetitive PEs affect episodic memory in brain and behavior. The current study investigated cerebral and behavioral effects of experiencing either multiple ('varying') or one single alternative version ('repetitive') of a previously encoded episode. Participants encoded a set of episodes ('originals') by watching videos showing toy stories. During scanning, subjects either experienced originals, one single or multiple alternative versions of the previously encoded episodes. Participants' memory performance was tested through recall of original objects. Varying and repetitive PEs revealed typical brain responses to the detection of mismatching information including inferior frontal and posterior parietal regions, as well as hippocampus, which is further linked to memory reactivation, and the amygdala, known for modulating memory consolidation. Further, experiencing varying and repetitive PEs triggered distinct brain areas as revealed by direct contrast. Amongst others, experiencing varying versions triggered activity in the caudate, a region that has been associated with prediction errors. In contrast, repetitive PEs activated brain areas which resembled more those for retrieval of originally encoded episodes. Thus, anterior and posterior cingulate cortex activation seemed to serve both reactivating old and integrating new but similar information in episodic memory. Consistent with neural findings, participants recalled original objects less accurately when only presented with the same, but not varying, PE during fMRI. The current findings suggest that repeated PEs interact more strongly with a recalled original episodic memory than varying prediction errors.

## INTRODUCTION

Retrieval can put a memory into a vulnerable state that allows for the integration of new information. This process opens a window to updated memories and returning them into a stable state over time (Lee et al., 2017). A driving factor of this remarkable plasticity of memory is probably prediction errors (PEs), i.e. the difference between our expectations and our actual experience (Exton-McGuinness et al., 2015; Fernández et al., 2016; Kim et al., 2014; Sinclair & Barense, 2019). These PEs allow the brain to update internal models of the world with new information in order to maintain accurate and functional predictions (Friston, 2002). Recurrent exposure to different PEs results in repeatedly violating adapted predictions as ever-changing information occur, whereas repeated exposure to the same PE results in greater familiarity with alternative information over time, successfully updating expectations and recall of PE-related input (Frank & Kafkas, 2021). While reconsolidating memories is a slow process over an extended period, adapting predictions and respective internal models of the world appears to be a rather dynamic, real-time process (Friston, 2002). In this way, PEs may fuel two types of processes: (i) adapting predictions during expectation violation, and (ii) updating stored memories in the long run. As our memory is constantly destabilized and restabilized, it is necessary to understand how the brain processes different types of competing information to maintain long-term valid predictions in the face of persistent change (Lee, 2009).

In the current study, we aimed to separate the neural signatures of episodic prediction violation from those of episodic prediction adaptation. To this end, we manipulated episodic cues to induce either varying PEs, i.e. multiple changes over time, or one single, repetitive PE. The basic idea was that the former condition should produce multiple predictions for an episode competing during re-experience of violated episodes, while the latter allows updated mnemonic predictions and, thus, facilitates subsequent memory modification in the long run (Brodt et al., 2016; Exton-McGuinness et al., 2015; Schiffer et al., 2013).

We adapted an episode-modification paradigm from our previous studies (Jainta et al., 2022). Participants encoded episodes from videos of short action stories in the lab. The subsequent day, they returned to an fMRI session in which we presented both the original videos as well as slightly modified versions of the first day's episodes. These modifications were generated by substituting one of the objects shown in the video repeatedly with the same (repetitive, *rep*) or with different objects over time (varying, *var*). On day three, we tested memory performance by assessing correct recall rates of originally encoded objects.

Regarding learning through PEs in episodic memory, the hippocampus (HC) has been suggested to be a core structure (Horner & Doeller, 2017; Stachenfeld et al., 2017) that processes mnemonic PEs (Bein et al., 2020; Long et al., 2016; Schiffer et al., 2012), especially when the experience is in some way related to expectation and not entirely novel (Chen et al., 2011; Duncan et al., 2009; Kumaran & Maguire, 2007).

Thus, HC is more active for competing than for novel events. Therefore, we expected HC would be activated by both repeated experience of repetitive and of varying alternative versions. Additionally, we expected a stronger effect for hippocampal activity during experience of multiple alternative versions compared to repeated presentation of a single alternative (*var* vs. *rep*) as the PE should decrease by repetitions for single alternatives.

Beyond HC, we expected episodic mismatches to come with increased activity in the inferior frontal sulcus (IFS; including BA 44 and BA 45), the parahippocampal gyrus (PHG), the fusiform gyrus (FG), intraparietal sulcus (IPS) and the occipitotemporal cortex (OTC) (Siestrup et al., 2022, 2023). Since the *rep* condition was designed to facilitate learning from PE whereas varying PE would lead to a prolonged phase of uncertainty, repetitive and varying PEs were expected to differently modulate activity in this neocortical network too. We expected that same network to be enhanced for varying (vs. repetitive) PE due to the repeatedly refreshed PE. In contrast, as we expected that the PE-related information of a single alternative version would lead to updating predictions regarding the repeatedly presented alternative, contrasting repetitive with varying PEs was expected to reveal brain regions that are typical for successful episodic retrieval, including the medial frontal cortex and precuneus / posterior cingulate cortex (Rugg & Vilberg, 2013; Schiffer et al., 2013). Notably, these cortical midline regions and a further one in the middle cingulate cortex were also more active for viewing originally encoded as compared to novel stories in several of our previous studies (Jainta et al., 2022; Siestrup & Schubotz, 2023). Moreover, medial frontal cortex, mCC and pCC were found to increase in activity for repeated presentations of modified stories in another study (Siestrup et al., 2022), but only when resulting in false memories in a post-fMRI survey. Therefore, these cortical midline areas were expected to become engaged by repetitive (vs. varying) presentations of a specifically modified story in case this manipulation would lead to changes in episodic memory.

In our previous studies, we had found that recurrent experience of the same expectation violation of originally encoded episodes led to higher acceptance for modified versions (false alarms) and slightly lower acceptance of originals (misses) (Jainta et al., 2022; Siestrup et al., 2022). We expected to see a replication of the effect that recall of originals is less accurate after being presented with a modified compared to a previously encoded version. However, the extent to which competing alternative episodes impair later retrieval of existing memories has been proposed to depend on two factors: (i) the co-existence of multiple alternatives for a single episode (Lee et al., 2017) and (ii) the memory strength of an alternative (Fernández et al., 2016). Hence, we could expect both varying and repetitive PEs to lead to impairments of memory performance.

# MATERIAL AND METHODS

## Participants

Forty-two right-handed subjects participated in one encoding session, one fMRI scan, and one post-fMRI memory test session. Five participants were excluded from the analyses: four due to excessive body movement during scanning, one did not complete the fMRI session. Therefore, 37 participants (23 females, 14 males) were included in the statistical analysis (*M* = 22.22, *SD* = 2.26 years old; range 18-28 years). In our previous work, this sample size yielded stable results by using an equivalent number of participants, experimental and statistical design (Jainta et al., 2022; Siestrup et al., 2023). Within the final data set, no person reported a history of neurological or psychiatric disorders or substance abuse. With regard to scores in the Edinburgh Handedness Inventory (Oldfield, 1971), all participants were right-handed while scores varied from +60 to +100. The study protocol was conducted in accordance with the Declaration of Helsinki and approved by the Local Ethics Committee of the University of Münster. Each subject gave written informed consent and received either course credits or reimbursement for their participation.

## Stimuli

The stimulus material consisted of 96 videos (mean duration = 12.75 s, *SD* = 1.81 s, range, 8.64 – 16.08 s) containing abstract action stories played with PLAYMOBIL® toys. Videos showed only hands and forearms of an actress and the toys, including characters, animals, man-made objects, vehicles, plants, and tools. These action stories comprised 6 to 9 action steps (*M* = 7.68 steps, *SD* = 0.7) and 4 to 7 separable toys (*M* = 5.77, *SD* = 0.79). The final set of stories was based on two previous studies of our lab (Jainta et al., 2022; Siestrup et al., 2023).

Within the total set of videos, 90 videos consisted of 18 stories each existing in five different versions, i.e. one original and four modified versions (for an example, please see Figure 1A). Modified versions could involve a change of the color or shape of an object or an object could be replaced by a new object. In each video, only two objects of the original story were manipulated for alternative versions. Modifications never occurred during the first or last two action steps of a story in order to ensure reactivation of the original story during the experiment. Four further videos served as novel videos (hereafter referred to as ‘novels’ or *nov*) and were presented for the first time during the fMRI session. The remaining two videos were only used for practice in the training and memory test session and did not appear in the scanning session.

Videos were filmed using a digital single-lens reflex camera (Nikon D5300). The camera was mounted above the center of the table and faced straight down. While we presented half of the videos from first person and half from third person perspective, this factor was irrelevant for the present study. Therefore, to balance perspective effects, video perspective remained the same throughout all sessions, and it was counterbalanced for all conditions and aggregated for all behavioral and functional analyses. During filming, all toy-based actions were performed on a matt white paper background by an actress wearing a black pullover and black rubber gloves. Videos had a resolution of 1920 x 1080 px and 25 frames per second. All videos were edited using Adobe Premiere Pro CC (Adobe Systems Software, Dublin, Ireland, Version 12.1.2) to ensure that each video started with seven frames showing only a white background and seven frames showing the final scene. Throughout the study, videos were presented using the stimulus presentation software Presentation (version 20.3 02.25.19, NeuroBehavioral Systems, Berkeley, CA, USA) at a visual angle of approximately 7.3° x 13°.

## Procedure

### Encoding

On the first of three consecutive days, participants took part in a ‘training session’ (approximately 1.5h), which we refer to as encoding session and took place at the same setup we used for filming (for a schematic overview, see Figure 1B). During encoding, participants were instructed to watch a set of short videos played with PLAYMOBIL® toys and describe them after watching.

In order to ensure that participants understood the task and description rules correctly, the session started with two practice trials. After the first practice video was presented and an ideal description example was given by the experimenter, the second practice video was presented and the participant had to give a detailed description of that practice story.

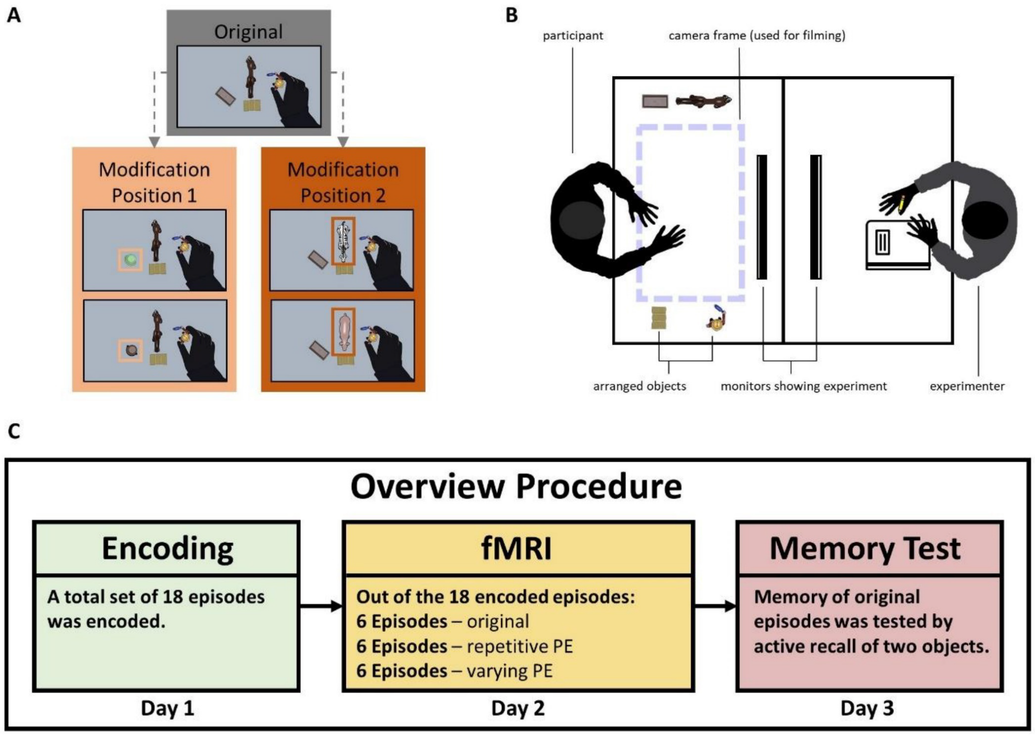

**Figure 1. (A)** Sample video frames for the original and four different modified versions for the episode 'brushing the horse'. In position 1 (left column), the brown horse trough was either replaced by a green (top) or a brown bucket (bottom). In position 2 (right column), the brown horse was either replaced by a black/white striped zebra (top) or a pink pig (bottom). Each violation only contained one replacement, meaning that either at position 1 or position 2 one object was replaced. **(B)** Original episodes were encoded at the same setup where the episodic videos were initially filmed. During the encoding session, videos were presented simultaneously to participant and experimenter. The experimenter listened carefully to the participant's description and took notes on attempts and mistakes made. Objects used in each video were placed around the camera frame (dashed lines) to facilitate understanding of the episode and visual recognition of object features. The schematic overview was adapted from Jainta et al. (2022). **(C)** Overview of the experimental procedure. All participants completed encoding (day 1), cued retrieval during fMRI (day 2), and a post-fMRI memory test (day 3). On day 1, participants encoded 18 episodes. On day 2, six of the encoded episodes were presented in their original, six in a single alternative version (repetitive), and six in multiple alternative versions. For the memory test on day 3, only the first two action steps of each episode were presented to trigger memory retrieval. Object recall was tested for the original object, encoded on day 1.

Subsequently, subjects watched each video five times during encoding before verbally describing the respective action story. The number of video presentations needed to correctly understand and describe each story was based on our previous studies (Jainta et al., 2022; Siestrup et al., 2023). After half of the videos, we included a short break to let participants rest for a few minutes. For description, participants had to follow specific rules in order to ensure correct understanding and interpretation of the stories. To facilitate interpretation and object descriptions, toys for each story were placed on the table, but not interacted with by participants during encoding. Each action step had to be described in the correct order and by describing each object that was placed in the scene or manipulated during the action step. In order to describe an object correctly, participants had to tell the experimenter the correct name and the main color of an object (e.g. ‘red table’). As characters usually include many different details, we instructed participants to name the color of the hair and the figure’s role in each scene. In case characters wore a hat, the hat and its color had to be given instead of the hair color (e.g. ‘the pirate with a black hat’). All objects characters carried in their hands had do be described additionally (e.g. ‘the pirate with a black hat and a silver pistol in their hand’). In case participants made a mistake during description, the experimenter interrupted them immediately, pointed out the error, and asked them to restart. As the experimenter corrected them verbally, subjects started the new description attempt without rewatching the video. The number of attempts to describe a story was not limited. In this way, we ensured participants’ attention and understanding of each story. On average participants needed 1.44 attempts per story and made 0.69 mistakes per story.

### Functional Magnetic Resonance Imaging Session

The fMRI took place one day after the encoding session and the experiment lasted approximately 52 minutes. During scanning, participants were presented either with original or modified videos reminiscent of the previously encoded episodes. Six episodes were only presented in the original version (hereafter referred to as ‘originals’ or *ori*), six only in one single modified version (repetitive version or *rep*), and six in different modified versions (varying versions or *var*). Episodes were assigned to each condition in a counterbalanced manner between participants, i.e., each video was presented equally often in each condition. Throughout the course of the experiment, each episode assigned to the *ori* or to the *rep* condition was presented eight times in the same version. As varying versions contained four different versions of a single story, each alternative video was presented twice, once in the first half of the experiment and once in the second half. Four videos served as novel stories (*nov*), each of them repeated four times during the fMRI session.

The fMRI experiment comprised 244 trials, consisting of 144 video trials showing episodes similar to the ones encoded, 32 video trials showing novels, 24 null events in which only a fixation cross was presented for 7 to 10 s, and 44 question trials of which half were to be accepted and the other half to be rejected. The experiment was divided into eight blocks, each containing 18 videos of previously encountered episodes, four novels, three null events, and five to six question trials. Thus, 25% of the videos were followed by a short description of the episodes’s scenery (e.g. ‘Under water?’) in order to ensure that participants attentively watched and recognized the action videos. Additionally, trials were variably jittered (0, 500, 1000, 1500 ms) and ended with a fixation cross (2 s after videos or 1 s after questions). The trial order was pseudorandomized to balance the order of presentation of the conditions within each block and balance transition probabilities between conditions. For a schematic overview of trials during fMRI, please see Figure 2.

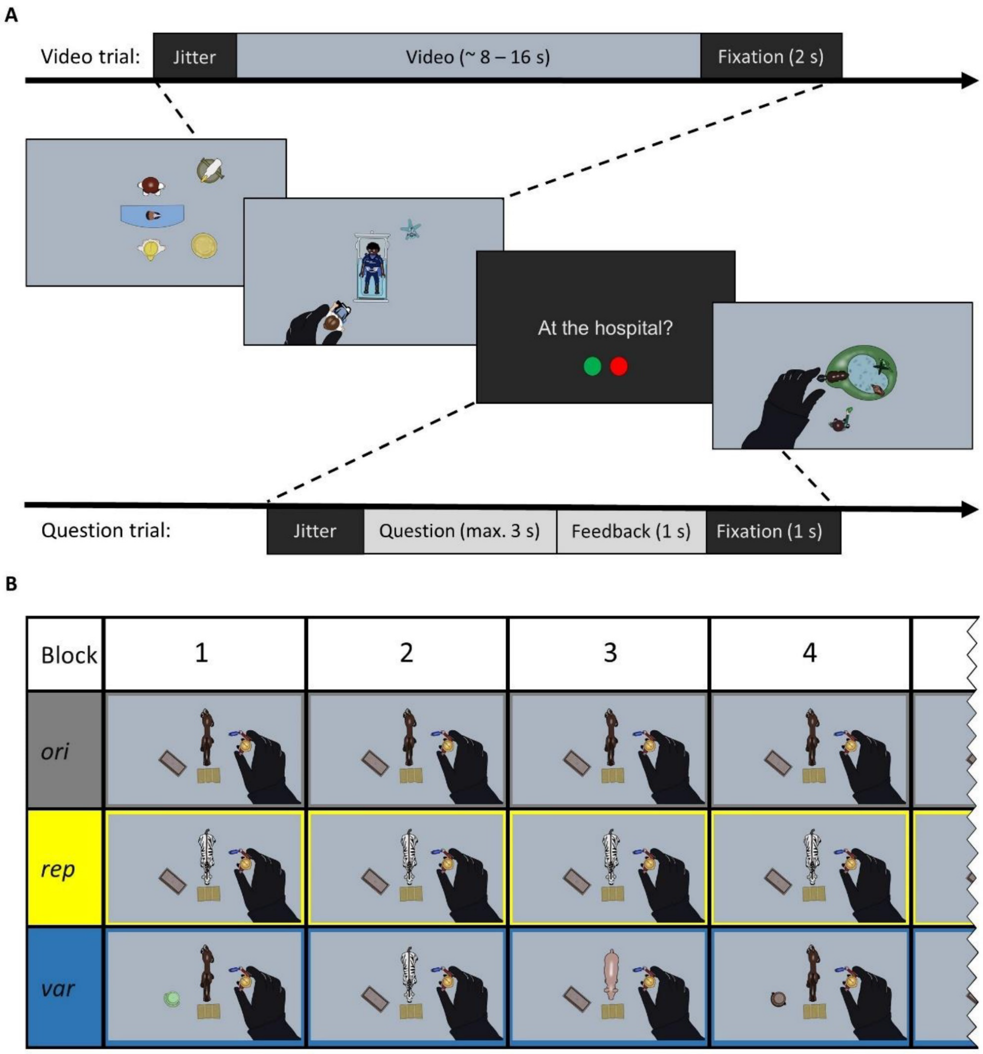

**Figure 2.** Schematic diagram of task during fMRI session. Video trials consisted of a variable jitter (0, 0.5, 1, or 1.5 s of fixation), a video showing an episode (~ 8 – 16 s), and an inter-stimulus interval (2 s of fixation). **(B)** Schematic overview of different video versions for a single episode (here: 'brushing the horse') when presented during scanning. Top row (white) showing number of each respective block during fMRI. Originals (dark grey) were always presented in the same version as previously encoded. When presented with a repetitive PE (yellow), subjects repeatedly experienced a single alternative version. For varying PEs (blue), participants watched multiple alternative versions of an encoded episode. Here, no alternative version was presented twice in a row. Please note, that only four out of eight video presentations are depicted here.

## Memory Test

One day after the fMRI session, participants came back to the behavioral lab in order to conduct a memory test. Participants were not informed in advance that their memory performance would be tested on day three, but rather that they would return for a computer task in which they would again be presented with videos showing PLAYMOBIL® stories.

The memory test took approximately 25 min. Subjects were instructed to watch short videos showing only the first two action steps of PLAYMOBIL® stories on a computer. In order to ensure that participants understood the task correctly, the session started with two practice trials including the practice videos from the encoding session. After each video, participants had to answer two questions using key responses and two questions asking for verbal recall of objects. Verbal responses were written down by the experimenter.

First, subjects had to rate whether they remembered the cued episode presented from the encoding session. Responses were given on a four-point Likert scale (1: *no*; 2: *rather no*; 3: *rather yes*; 4: *yes*) using four marked keys on the computer's keyboard.

Second, participants were asked how vivid their memory is. Here, participants were instructed to rate vividness based on how detailed their mental image of the episode is as well as how strong their feeling of mentally moving their arms in accordance with the presented videos is. Responses were measured on a six-point Likert scale from 1 (= *not vivid at all)* to 6 (= *very vivid*). Participants had to press one of six marked keys on the computer's keyboard. There was no time restriction for responses, but extreme outliers were removed as described in the following section.

Third, participants were presented with a screenshot showing a later action step of the corresponding episode in which the first of the two potentially violated objects appeared. This object was masked using a black box showing the number '1' indicating position one. Then, participants were asked to answer which object was placed in the episode at position one. After verbally responding, participants had to press the space bar to continue with the next screenshot. The second screenshot showed the action steps in which the second potentially violated object was presented for the first time. In order to avoid feedback on previous responses, the object from the previous screenshot remained masked, but this time without an indexing number. The newly added black box contained the number '2' indicating position two and participants were asked to name the object that was placed at that particular position. Participants were instructed to describe recalled objects and characters following the rules from the encoding session. Thus, after two practice trials participants had to respond to a total of 22 videos, i.e. 18 originally encoded and 4 of the novel videos.

### Functional Magnetic Resonance Imaging Acquisition and Preprocessing

MRI scans were performed on a 3-Tesla Siemens Magnetom Prisma MR tomograph using a 20-channel head coil and took place one day after the encoding session. Participants laid down in a supine position, their index and middle finger positioned on the two buttons on the response box. Using form-fitting cushions, we minimized head and arm movements by tightly fixating subjects' heads and arms. Additionally, participants were provided with earplugs and headphones to attenuate scanner noise. For stimuli presentation, the experiment was projected on a screen behind the fMRI machine which participants saw through an individually adjusted mirror on the head coil.

First, high-resolution anatomical images (T1 weighted) were created with a 3D multiplanar rapidly acquired gradient-echo (MPRAGE) sequence (192 slices, thickness = 1 mm, repetition time (TR) = 2130 ms, echo time (TE) = 2.28 ms, flip angle = 8°, field of view (FoV) = 256 x 256 mm$^2$). Whole-brain functional images were acquired in interleaved order along the AC-PC plane using a gradient-echo echoplanar imaging (EPI) sequence to measure blod-oxygen-level-dependent (BOLD) contrast (33 slices, thickness = 3 mm, repetition time (TR) = 2000 ms, echo time (TE) = 30 ms, flip angle = 90°, field of view (FoV) = 192 x 192 mm$^2$).

Brain image preprocessing and statistical analyses were conducted using SPM12 (Wellcome Trust, London, England) implemented in MATLAB (Version R2021b, The MathWorks Inc., Natick, MA, USA). For functional images, we applied slice time correction to the middle slice to correct for differences in slice acquisition time, movement correction and realignment to the mean image, and co-registration of functional and structural scans. Further, we normalized functional and structural images into standard MNI space and performed spatial smoothing using a Gaussian kernel of full-width at half maximum (FWHM) of 8 mm. A 128 s high-pass temporal filter was applied.

## Statistical Data Analysis

### Behavioral Data Analysis

The behavioral data from the fMRI session and the memory test were analyzed using RStudio (R Core Team, 2020; version 1.3.1073). Behavioral performance during fMRI was assessed by correct response rates and RTs on correctly answered question trials. For the memory test, the average ratings and RTs were analyzed using a repeated measures analysis of variance (rmANOVA). Regarding RTs, we only selected correct answers based on the familiarity question. In the next step, the participants were sequentially presented with two images in which an object's position was hidden behind a black box. Here, subjects had to verbally recall the respective object from the training session. The mean recall rates (achieved score/maximum score) and mean RTs were evaluated using a rmANOVA. For mean RTs, we only used trials in which participants made no mistake in recalling the object's attributes (name and color). For mean recall rates, we investigated differences in memory performance for previously encoded videos after experiencing an original version, a repetitive object change, or a varying object change during fMRI.

To investigate mean recall rates (achieved score/maximum score) and mean RTs, Bayesian hierarchical generalized models, brms (Bürkner, 2017), and rStan (https://mc-stan.org/) were used. Two models were calculated. In these models, the recall rate (Eq. 1) and RTs (Eq. 2) were predicted by the type of modification and sequential position of the object. Further, three random intercepts were assumed for trial, video, and subject. Since in both models, the output was not normally distributed, by checking the Cullen Frey graph, appropriate generalized models were employed instead of normal linear ones. More specifically, for recall rate, a beta-binomial model, and for RTs, a shifted lognormal model was used.

$$Recall\ Rate\ (trials|4){\sim}\ Modification * Position + (1|Trial) + (1|Video) + (1|ID)\ \ (Eq.1)$$

$$RT \sim Modification * Position + (1|Trial) + (1|Video) + (1|ID)\ \ (Eq.2)$$

For both models, uninformative priors were selected, as suggested by previous studies (Bürkner, 2017; Dienes & Mclatchie, 2018). For recall rates, we used *N* (0,2.5) as uninformative priors for β coefficients, *student_t* (3, 0, 2.5) for intercept, *student_t* (3, 0, 2.5) for sigma, and *uniform* priors for ndt. For RTs, we applied *N* (0,0.5) as uninformative priors for β coefficients, *student_t* (3, 8.7, 2.5) for intercept, *student_t* (3, 0, 2.5) for sigma, and *gamma* (0.01,0.01) for phi. Both models were calculated with four chains, each having 5000 iterations with 2000 warmups. Both models converged with Rhat = 1.00 (i.e., the potential scale reduction factor on split chains). Further, all parameters were sampled sufficiently, as all tail and bulk effective sample sizes were over 2000.

Hypotheses were tested using the hypothesis package included in brms (Bürkner, 2017). Based on recent literature, we considered *Bayes factors* (*BF*) > 3 and *BF* < $\frac{1}{3}$ as significant evidence for accepting and rejecting the tested hypothesis, respectively (van Doorn et al., 2021). One-sided hypotheses (denoted by: $BF_{+0}$, $BF_{-0}$) were the comparison of the posterior probability of hypotheses against their alternative; two-sided tests (denoted by: $BF_{01}$) were the comparison between hypotheses and their alternative computed via the Savage-Dickey density ratio method.

Prior to conducting the analyses, data distribution was tested by using the Shapiro-Wilk Test and excluded outliers as defined by values higher than the 75% quartile +3 x interquartile range or lower than the 25% quartile -3 x interquartile range. In cases where data were normally distributed or could be logarithmically transformed to fit normal distribution (RTs), we used parametric rmANOVA. When data were not normally distributed, we opted for a non-parametric rmANOVA based on aligned rank data (package *ARTool*; Wobbrock, Findlater, Gergle, & Higgins, 2011) and calculated post-hoc pairwise comparisons using the Wilcoxon signed-rank test.

For all rmANOVAs and respective post hoc testing, the significance level was set to $p < .05$. To address multiple comparisons, *p* values were adjusted according to the Bonferroni-Holm correction (Holm, 1979). As descriptive statistics, we report mean values and standard errors of the mean.

### fMRI design specifications

For the statistical analysis of the fMRI data with SPM12, we used the general linear model (GLM) for serially autocorrelated observations based on least-squares estimation (Friston et al., 1994; Worsley & Friston, 1995). The GLM convolved a total of 15 regressors with a canonical hemodynamic response function. We included six regressors containing three predictors (*ori, var, rep)* and three parametric modulators (*par_ori, par_var, par_rep)* for the experimental conditions. Parametric modulators were included to model brain activity of repeated presentation over time. The 32 *novel* trials were modeled as one regressor as well (*nov*). All video trials were modeled as epochs containing the full video duration and onsets time-locked to the beginning of the video. Additionally, two regressors modeled the 24 null events and the 44 question trials. Null events were modeled as epochs (7-10 s) and questions were modeled as events. Six regressors of no interest were included for the subject-specific motion parameters obtained from realignment.

On the first level of the analysis, gray matter masking was implemented using the smoothed individual normalized gray matter image (8-mm FWHM). In order to create binary masks, smoothed images were thresholded at 0.2 using ImCalc in SPM12. For the second-level group analysis, one-sample *t*-tests were performed to evaluate brain activation patterns across participants. We applied a threshold of $p < .001$ on the whole-brain level to identify significant effects. To control for false positive results, we applied false discovery rate (FDR) correction at $p < .001$ to resulting *t*-maps.

Our GLM aimed to examine the effects of varying and repetitive mnemonic PEs. Therefore, we calculated the first-level *t*-contrasts *var* > *ori* and *rep* > *ori* to analyze brain activity in response to the specific PE types. To investigate shared effects of both modification types, we further calculated a conjunction of modification types (*var* > *ori*) ∩ (*rep* > *ori*). In order to gain a more detailed view of specific brain responses due to the respective modification type, we further calculated the direct contrasts *var* > *rep* and *rep* > *var.* Regarding the attenuation effects of repeated video presentation over time, we calculated the contrasts for parametric modulators against implicit baseline (*par_ori, par_var, par_rep*) to identify brain regions in which the BOLD response decreased with the number of presentations. To demonstrate successful retrieval of encoded episodes and replicate our previous findings, we calculated first-level *t*-contrasts for each episodic condition versus novels (*ori* > *nov*).

In addition, we explored hippocampal activity for cued memory retrieval of original and violated episodic memories, i.e. repetitive and varying PEs. Regarding recent research (Bein et al., 2020), we were interested in the specific contributions of corno ammonis (CA) subregions (CA1 and CA3) during re-experience of repetitive and varying PEs. To this end, anatomical ROIS of the left and right hippocampus were imported from the Julich-Brain Cytoarchitectonic Atlas (Amunts et al., 2020). To account for potential overlaps in ROIs, a threshold of 0.2 was implemented in ImCalc and final ROIs were created using the MarsBaR toolbox (Brett et al., 2002) in SPM12. Following Bein et al. (2020), CA3 ROI included probabilistic maps of CA2 subregion and the dentate gyrus. We extracted mean beta values for left and right hippocampal subfields for the regressors *ori, var,* and *rep.* To extract mean beta values, we used the MarsBaR Toolbox (Brett et al., 2002). For statistical analysis, we used a three-way rmANOVA with the factors MODIFICATION$_{\text{FMRI}}$ (*var, rep, ori*), HEMISPHERE (*left, right*), and SUBFIELD (*CA1, CA3*). Post-hoc comparisons were conducted with pairwise *t*-tests (two-tailed), a significance level of $\alpha = 0.05$, and Bonferroni-Holm-corrected for multiple comparisons (Holm, 1979).

## RESULTS

### Behavioral results of the fMRI session (Cover Task)

During the scanning phase, participants had to answer questions about the content of the video. Questions did not address information that could be modified due to the change of an object. After excluding trials in which no response was given (1.23 %), the average RT was 922 ms (± 16 ms), while the average error rate was low (0.058 ± 0.006) indicating that participants attentively observed and recognized the action stories.

To analyze behavioral performance during fMRI, we conducted a nonparametric rmANOVA on error rates with the factor CONDITION$_{\text{FMRI}}$ (*ori, var, rep, nov*). We found a significant main effect of condition ($F(3, 108) = 11.3$, $p < .001$, $\eta^2p = .24$). Bonferroni-Holm corrected post hoc analyses with Wilcoxon pairwise tests (two-tailed) revealed significant differences between *ori* ($M_{ori} = .033 \pm .008$) and *nov* ($M_{nov} = .13 \pm .019$; $Z = -3.9, p < .001$) as well as between *var* ($M_{var} = .067 \pm .012$) and *nov* ($M_{nov} = .13 \pm .019$; $Z = -2.7, p = .002$). In addition, there was a trend for the comparison between *rep* ($M_{rep} = .078 \pm .012$) and *nov* ($M_{nov} = .13 \pm .019$; $Z = -2.6, p = .02$). All together indicate that episodes were better recognized than novels. Further, we found a significant difference between *ori* ($M_{ori} = .033 \pm .008$) and *rep* ($M_{rep} = .078$ $.012$; $Z = -3.09, p = .002$) and a trend for the comparison between *ori* ($M_{ori} = .033 \pm .008$) and *var* ($M_{var} = .067 \pm .012$; $Z = -2.1, p = .036$) suggesting that participants performed best when videos showed original content from the training session.

With regard to RTs on correct responses, we found a significant main effect of CONDITION$_{FMRI}$ ($F(3, 108) = 4.612$, $p = .004$, $\eta^2p = .114$). Bonferroni-Holm corrected post hoc analyses with pairwise comparisons (two-tailed) revealed a significant difference between *var* ($M_{var} = 893$ ms ± 31 ms) and *nov* ($M_{nov} = 961$ ms ± 35 ms; $t(36) = -3.48$, $p = .001$) and a trend between *ori* ($M_{ori} = 916$ ms ± 30 ms) and *var* ($M_{var} = 893$ ms ± 31 ms; $t(36) = 2.19$, $p = .03$).

## fMRI Results

### Effects of Varying and Repetitive Expectation Violation

In order to identify specific brain regions related to varying PEs and repetitive PEs, we first calculated whole-brain contrasts for modified versus original videos (*var* > *ori*, *rep* > *ori*).

When comparing varying versions with original episodes (*var* > *ori*), recurrent experience of prediction errors activated dorsal premotor cortex (PMd), inferior frontal junction (IFJ), inferior frontal sulcus (IFS), and gyrus (IFG) including Brodmann Area (BA45), lateral occipital cortex (LOC), and caudate. Superior parietal lobe (SPL), precuneus (PCUN), and superior temporal sulcus (STS) showed increased activity in right hemisphere.

For repetitive PEs versus baseline episodic retrieval (*rep* > *ori*), we found increased activity in bilateral PMd, IFS (extending into IFG), SMA, superior occipital lobe (SOL), hippocampus (HC), and amygdala, while unilateral activation was observed in right SPL, right anterior PCUN, right somatosensory cortex, left inferior parietal lobe (IPL), and left middle occipital lobe (MOL).

To detect shared brain activation in varying PEs and repetitive PEs, a conjunction of *var* > *ori* and *rep* > *ori* contrasts was calculated. Modified compared to original videos triggered bilaterally enhanced brain activation in PMd, IFS, IFG, SPL, intraparietal sulcus (IPS), HC, amygdala, as well as unilaterally right superior frontal sulcus (SFS), right anterior PCUN, and right posterior PCUN (Table 1, Figure 3).

To characterize differences between varying and repetitive PEs, we further calculated direct contrasts between the two types of PEs (*var* > *rep*, *rep* > *var*). In versions containing varying versus repetitive PEs (*var* > *rep*), significant brain activation included LOC, left SPL, left IPS, left IFG (BA 44), and right MFG extending into IFG (BA 45) (Table 2, Figure 4C).

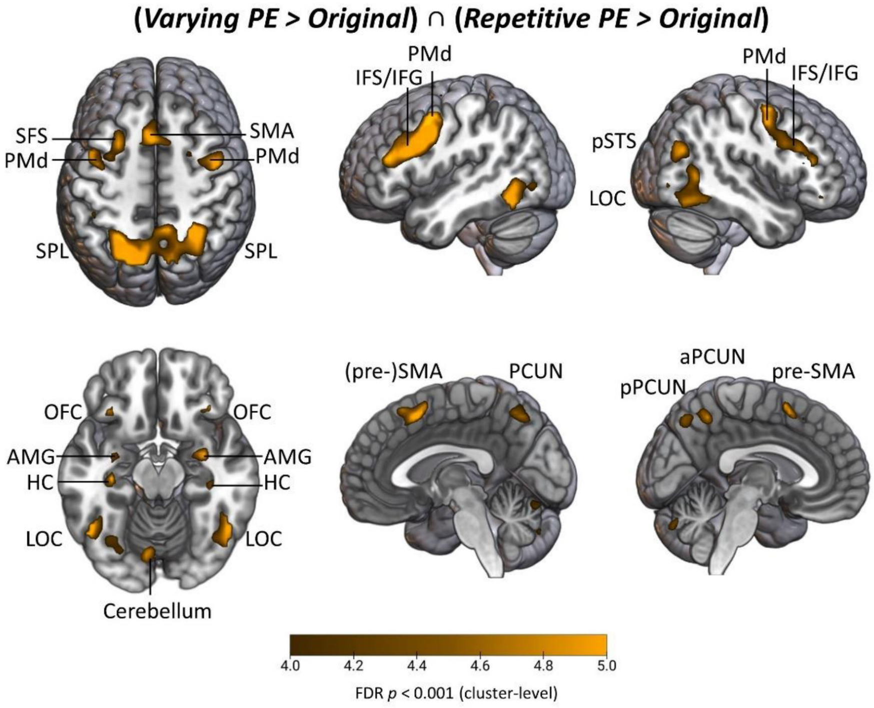

**Figure 3.** Shared brain activation to repetitive and varying episodic prediction errors. FDR-corrected *t*-map ($p < .001$) for the (*Varying PE > Original)* ∩ (*Repetitive PE > Original*) contrast. SFS = superior frontal sulcus; PMd = dorsal premotor cortex; SPL = superior parietal lobe; IFS/IFG = inferior frontal sulcus/gyrus; PTL = parietal temporal lobe; LOC = lateral occipital cortex; OFC = orbitofrontal cortex; AMG = amygdala; HC = hippocampus; SMA = supplementary motor area; p/aPCUN = posterior/anterior precuneus.

**Table 1. Peak activation of second-level whole-brain analysis for shared brain activity of prediction violation.**

| Area | H | Cluster extent | MNI Coordinates | | | Z |
|---|---|---|---|---|---|---|
| | | | x | y | z | |
| (*var* > *ori*) ∩ (*rep* > *ori*) | | | | | | |
| SMA / Pre-SMA | L | 110 | -3 | 14 | 50 | 4.90 |
| | R | l.m. | 3 | 8 | 59 | 4.54 |
| PMd | R | 380 | 45 | -4 | 56 | 4.94 |
| Inferior frontal sulcus | R | l.m. | 42 | 23 | 23 | 4.42 |
| | | l.m. | | | | |
| IFG (BA 45) | R | l.m. | 54 | 26 | 23 | 4.14 |
| Superior frontal sulcus | R | l.m. | 24 | 5 | 50 | 3.97 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Intraparietal sulcus | L | 2094 | -24 | -82 | 38 | 5.72 |
| | R | l.m. | 33 | -82 | 29 | 5.21 |
| Superior parietal lobe | R | l.m. | 15 | -79 | 47 | 5.51 |
| | L | l.m. | -24 | -67 | 41 | 5.43 |
| pSTS | R | l.m. | 57 | -46 | 17 | 4.78 |
| Dorsal posterior precuneus | R | 19 | 9 | -70 | 47 | 4.35 |
| Anterior precuneus | R | 17 | 9 | -52 | 50 | 4.60 |
| Precuneus | L | l.m. | -6 | -64 | 50 | 4.62 |
| Superior frontal sulcus | L | 694 | -48 | 11 | 29 | 5.33 |
| PMd | L | l.m. | -36 | 2 | 59 | 4.94 |
| Inferior frontal sulcus | L | l.m. | -45 | 29 | 20 | 4.73 |
| LOC | L | 260 | -54 | -58 | -10 | 5.70 |
| Fusiform gyrus | L | l.m. | -30 | -63 | -13 | 4.07 |
| Orbitofrontal cortex | R | 86 | 36 | 29 | -10 | 5.20 |
| | L | 51 | -36 | 26 | -13 | 4.76 |
| Anterior dorsal insula | L | l.m. | -27 | 26 | 2 | 4.56 |
| Hippocampus | L | 42 | -33 | -22 | -13 | 4.99 |
| Amygdala | L | l.m. | -33 | -7 | -13 | 4.22 |
| | R | 66 | 30 | -4 | -19 | 4.84 |
| Hippocampus | R | l.m. | 36 | -28 | -13 | 4.49 |
| Cerebellum | L | 44 | -9 | -76 | -16 | 4.84 |

L, left; R, right; H, hemisphere; MNI, Montreal Neurological Institute; l.m., local maximum; SMA, supplementary motor area; PMd, dorsal premotor cortex; IFS, inferior frontal sulcus; IFG, inferior frontal gyrus; BA, Brodmann Area. FDR-corrected at $p < .001$.

The reversed contrast (*rep* > *var*) revealed increased activity in ventral PM (PMv), pregenual anterior cingulate cortex (pgACC), posterior cingulate cortex (pCC), and cuneus (CUN) in both hemispheres. Unilaterally, we found increased brain activity in right anterior dorsolateral prefrontal cortex (dlPFC), right subgenual ACC, right posterior cingulate cortex (pCC), right posterior STS, right lingual gyrus (LG), and right mid insula (mINS) (Table 3, Figure 4A).

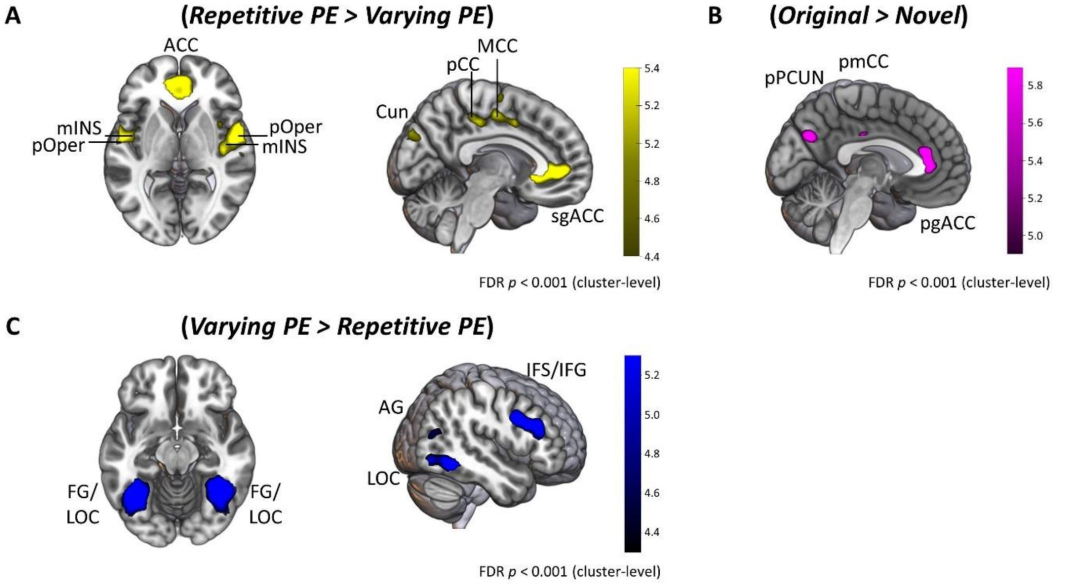

**Figure 4.** Distinct whole-brain activation for different types of cued episodes. (A) FDR-corrected *t*-map ($p < .001$) for the *Repetitive PE* > *Varying PE* contrast. (B) FDR-corrected *t*-map ($p < .001$) for the *Original* > *Novel* contrast. (C) FDR-corrected *t*-map ($p < .001$) for the *Varying* > *Reptitive* contrast. mINS = mid insula; pOper = parietal operculum; Cun = cuneus; pCC = posterior cingulate cortex; mCC = mid-cingulate cortex; ACC = anterior cingulate cortex; pPCUN = posterior precuneus; FG = fusiform gyrus; LOC = lateral occipital cortex; AG = angular gyrus; IFS/IFG = inferior frontal sulcus/gyrus.

**Table 2. Peak activations of second-level whole-brain analysis of varying compared to repetitive PEs.**

| Area | H | Cluster extent | MNI Coordinates | | | Z |
|---|---|---|---|---|---|---|
| | | | x | y | z | |
| (*var* > *rep*) | | | | | | |
| Superior parietal lobe | L | 178 | -27 | -67 | 56 | 5.06 |
| Intraparietal sulcus | L | l.m. | -27 | -55 | 44 | 4.63 |
| Superior parietal lobe | R | 481 | 33 | -55 | 41 | 6.18 |
| Occipitotemporal cortex | R | l.m. | 39 | -73 | 20 | 5.10 |
| Inferior frontal junction | R | 369 | 39 | 5 | 32 | 6.02 |
| MFG e.i. IFG (BA 45) | R | l.m. | 51 | 29 | 26 | 5.52 |
| PMd | R | l.m. | 36 | -1 | 53 | 5.07 |
| MFG | R | l.m. | 39 | 8 | 62 | 4.86 |
| Inferior frontal junction | L | 50 | -42 | 5 | 32 | 4.90 |
| IFS/IFG (BA 44) | R | 22 | 51 | 23 | 23 | 5.25 |
| Fusiform gyrus | R | 385 | 36 | -52 | -10 | 6.32 |
| Inferior occipital lobe | R | l.m. | 36 | -64 | -7 | 5.86 |
| Lateral occipital cortex | R | l.m. | 48 | -73 | -10 | 4.48 |
| Fusiform gyrus | L | 374 | -39 | -52 | -10 | 5.87 |
| Lateral occipital cortex | L | l.m. | -42 | -67 | -7 | 5.52 |
| Cerebellum | L | 111 | -9 | -73 | -25 | 5.37 |
| | R | 18 | 3 | -55 | -37 | 4.39 |

L, left; R, right; H, hemisphere; MNI, Montreal Neurological Institute; l.m., local maximum; MFG, middle frontal gyrus; IFG, inferior frontal gyrus; BA, Brodmann Area; PMd, dorsal/ventral premotor cortex; IFS, inferior frontal sulcus. FDR-corrected at $p < .001$.

**Table 3. Peak activations of second-level whole-brain analysis of repetitive compared to varying PEs.**

| Area | H | Cluster extent | MNI Coordinates x | y | z | Z |
|---|---|---|---|---|---|---|
| (*rep* > *var*) | | | | | | |
| PMd | L | 16 | -33 | -13 | 71 | 4.79 |
| M1 | L | 63 | -39 | -22 | 53 | 4.57 |
| SMA / mid-cingulate cortex | L/R | 185 | 0 | -10 | 47 | 5.25 |
| pCCd | R | 26 | 9 | -28 | 44 | 4.51 |
| Anterior dlPFC | R | 27 | 36 | 44 | 32 | 5.08 |
| Cuneus | R | 76 | 9 | -91 | 32 | 4.36 |
| | L | l.m. | -3 | -85 | 26 | 4.34 |
| Parietal operculum | L | 385 | -60 | -28 | 20 | 5.43 |
| PMv | L | l.m. | -54 | -4 | 8 | 5.08 |
| Mid insula | L | l.m. | -36 | 5 | 11 | 4.89 |
| PMv | R | 497 | 54 | -1 | 5 | 5.48 |
| Parietal operculum | R | l.m. | 60 | -22 | 20 | 4.77 |
| Mid insula | R | l.m. | 36 | 8 | 11 | 5.16 |
| ACC | L | 382 | -12 | 38 | -4 | 5.61 |
| subgenual ACC | R | l.m. | 3 | 20 | -4 | 5.43 |
| pregenual ACC | R | l.m. | 6 | 44 | -1 | 5.29 |
| | L | l.m. | -3 | 32 | 8 | 5.18 |

L, left; R, right; H, hemisphere; MNI, Montreal Neurological Institute; l.m., local maximum; PM(d/v), (dorsal/ventral) premotor cortex; M1, primary motor cortex; pCCd, dorsal posterior cingulate cortex; dlPFC, dorsolateral prefrontal cortex; SMG, supramarginal gyrus; pSTS, posterior superior temporal sulcus; ACC, anterior cingulate gyrus. FDR-corrected at $p < .001$.

## Parametric Effects of Episode Repetition

In line with our main research question, we investigated the effects of repeated presentation of one single (*rep*) or multiple alternative versions (*var*) of a re-activated episode. To analyze parametric decrease during repeated exposure to prediction errors over time, we first calculated the contrasts for parametric modulators against implicit baseline (*par_ori, par_var, par_rep)* on the whole-brain level. Please note that as effects of parametric modulators did not survive FDR-correction at < *.001*, we applied an FDR correction at the significance level of < .05. For original videos (*par_ori*), we found a parametric decrease in bilateral ventral posterior PCUN (left: x = -9, y = -64, z = 38, $Z$ = 4.79; right: x = 15, y = -61, z = 35, $Z$ = 4.53) while for varying videos (*par_var*) a decrease was located in left ventral posterior PCUN (level x = -3, y = -67, z = 41, $Z$ = 4.79) and left IPL (x = -42, y = -67, z = 50, $Z$ = 3.98). With regard to repetitive PEs (*par_rep*), we found significant attenuation in bilateral PCUN (left: x = -9, y = -64, z = 38, $Z$ = 4.13; right: x = 12, y = -67, z = 41, $Z$ = 4.13), bilateral IPL (left: x = -39, y = -58, z = 47, $Z$ = 4.21; right: x = 45, y = -58, z = 53, $Z$ = 4.79), left Thalamus (x = -3, y = -13, z = 2, $Z$ = 4.24) and right posterior mCC (pmCC) (x = 3, y = -31, z = 32, $Z$ = 4.08).

### Explorative ROI-analysis

Further, we used anatomical ROIs to investigate the specific contributions of hippocampal subfields during re-experience of originals and violated episodes. As recent literature (Bein et al., 2020) highlighted the role of hippocampal subfields in successful predictions and during experience of mnemonic PEs, we explored potential effects of small regions in our paradigm. Specifically, we tested whether CA1 and CA3 led to distinct brain responses during experience of repetitive and varying PEs. In order to further account for effects based on lateralization, we performed a three-way rmANOVA with the factors MODIFICATION$_{\text{FMRI}}$ (*var, rep, ori*), HEMISPHERE (*left, right*) and SUBFIELD (*CA1, CA3*). During cued retrieval of episodes, we found significant main effects of MODIFICATION$_{\text{FMRI}}$ ($F(2, 72) = 19.73, p < .001$, $\eta^2p = .354$) and HEMISPHERE ($F(1, 36) = 13.69, p < .001$, $\eta^2p = .276$). The main effect of SUBFIELD was not significant ($F(1, 36) = 0.51, p = .48$, $\eta^2p = .014$). Post hoc two-sided testing revealed that originals ($M$ = .007 +- .007) triggered significantly less activation of the hippocampal subfields compared to varying PEs ($M$ = .033 +- .007; $t(36) = -4.69$ $p < .001$, *Cohen's d* = .31) and repetitive PEs ($M$ = .035 +- .007; $t(36) = -5.08$ $p < .001$, $d = .33$). Repetitive and varying PEs did not trigger distinct activation in HC ($t(36) = 0.45$ $p = .06$, $d = .02$). Additionally, HC in the left hemisphere ($M$ = .046 +- .005) was stronger activated than in the right hemisphere ($M$ = .005 +- .005; $t(36) = 4.32$ $p < .001$, $d = .5$). After correcting for multiple comparisons, we found a marginally significant interaction between the factors MODIFICATION and SUBFIELD ($F(2,72) = 3.54, p = .03$, $\eta^2p = .09$). Regarding activation of CA1, repetitive PEs ($M$ = .036 +- .01; $t(36) = 5.07$ $p < .001$, $d = .35$) and varying PEs ($M$ = .035 +- .01; $t(36) = 4.8$ $p < .001$, $d = .33$) each triggered stronger activation than originals in CA1 ($M$ = .007 +- .01). Compared to originals ($M$ = .008 +- .01), we found CA3 to be more activated during re-experience of both repetitive PEs ($M$ = .034 +- .01; $t(36) = 5.04$ $p < .001$, $d = .32$) and varying PEs ($M$ = .032 +- .01; $t(36) = 4.52$ $p < .001$, $d = .29$). We did not find any further two-way or three-way interactions.

### Replication of former findings – Effects of Episodic Memory Retrieval

With regard to replicating results from our previous studies and demonstrating successful episodic retrieval, we contrasted original and new videos (*ori* > *nov*). Episodic retrieval triggered significant brain activation bilaterally in pgACC, BA 10, pmCC, IPL, and unilaterally in left posterior PCUN (Table 4, Figure 4B).

**Table 4. Peak activations of second-level whole-brain analysis of originals compared to novels.**

| Area | H | Cluster extent | MNI Coordinates | | | Z |
|---|---|---|---|---|---|---|
| | | | X | y | z | |
| (*ori* > *nov*) | | | | | | |
| pregenual ACC (BA 24) | L | 200 | -6 | 35 | 8 | 7.03 |
| | R | l.m. | 9 | 35 | 2 | 6.38 |
| BA 10 | L + R | l.m. | 0 | 47 | 8 | 4.59 |
| Ventral posterior PCUN | L | 95 | -9 | -64 | 29 | 5.88 |
| Angular Gyrus | L | 28 | -51 | -58 | 50 | 5.29 |
| | R | 16 | 54 | -58 | 47 | 5.11 |
| pmCC (BA 23) | L + R | 24 | 0 | -22 | 35 | 5.20 |

L, left; R, right; MNI, Montreal Neurological Institute; l.m., local maximum; ACC, anterior cingulate cortex; BA, Brodmann Area; PCUN, precuneus; pmCC, posterior mid-cingulate cortex. FDR-corrected at $p < .001$.

## Memory Test Results

To investigate the effects of varying and repetitive PEs on behavioral memory performance, we concentrated our analysis of ratings, RTs, and original object recall on videos that have been encoded during the training session. Object modifications never occurred in the first two action steps of an episode to ensure episodic memory retrieval during fMRI. We decided to not include novels in the analysis as they were presented the first time during the fMRI session which made it more difficult for participants to correctly encode object details compared to the training session biasing potential effects rather through visual than mnemonic accessibility. Further, we showed in our previous studies (Jainta et al., 2022; Siestrup et al., 2023) that memory performance for encoded episodes was more accurate than for novels.

### Memory Performance on Original Object Recall

For recall rate, the results of the model (Eq. 1) showed that memory performance was less accurate when presented with the same PE compared to re-experience of originals ($H_{-}$: *rep* < 0; mean = -0.43 [-0.74,-0.11], *E.E.* = 0.19, ***p.p.*= .99**, **$BF_{-0}$= 70.86**). However, for the experience of varying PEs compared to originals, the models did not show substantial evidence for accepting the tested hypothesis ($H_{-}$: *var* < 0; mean = -0.11 [-0.43,0.21], *E.E.* = 0.21, *p.p.*= .71, $BF_{-0}$ = 2.48). When directly comparing the same and varying PEs, the same PEs resulted in less accurate retrieval of originally encoded versions ($H_{-}$: *rep – var* < 0; mean = -0.31 [-0.63,0.00], *E.E.* = 0.19, ***p.p.*= .95**, **$BF_{-0}$ = 19.34**).

For the model of RTs (Eq. 2), we found substantial evidence that repeated presentation of the same PE resulted in slower retrievals than originals ($H_{+}$: *rep* > 0; mean = 0.09 [0.01,0.16], *E.E.* = 0.05, ***p.p.*= .97**, **$BF_{+0}$= 35.59**). Again, for repeated presentation with videos showing varying PEs, we did not find substantial evidence for the tested hypothesis ($H_{+}$: *var* > 0; mean = -0.01 [-0.07,0.08], *E.E.* = 0.04, *p.p.*= .56 $BF_{+0}$ = 1.28). Re-experiencing the same PE during scanning further led to slower retrieval during the memory test when compared to varying PEs ($H_{+}$: *rep – var* > 0; mean = 0.08 [0,0.15], *E.E.* = 0.05, ***p.p.*= .96**, **$BF_{+0}$ = 21.9**).

To account for the potential effects of object position within each episode, we included Position as a predictor in our models (Eq. 1 and Eq. 2). Regarding original object retrieval, we found substantial evidence that less accurate recalls occurred for objects located in Position 2 compared to Position 1 ($H_{-}$: Pos2 < 0; mean = -0.34 [-0.65,-0.03], *E.E.* = 0.19, ***p.p.*= .97**, **$BF_{-0}$ = 27.92**). Furthermore, we found substantial evidence that object retrieval from Position 1 and 2 was similarly accurate for the recurrent presentation of the same PE during fMRI compared to the originals ($H_0$: *rep*:Pos2 = 0; mean = -0.28 [-0.22,0.79], *E.E.* = 0.26, *p.p.*= .85, **$BF_{01}$ = 5.45**). In addition, we found substantial evidence for the similarly accurate object retrieval from Position 1 and 2 after re-experiencing repetitive compared to varying PEs in the scanner ($H_0$: *rep*:Pos2 – *var*:Pos2 = 0; mean = -0.23 [-0.75,0.29], *E.E.* = 0.27, *p.p.*= .91, **$BF_{01}$ = 9.57**). Regarding RTs, our models provided substantial evidence that objects from Position 2 were recalled slower than objects from Position 1 ($H_{+}$: Pos2 > 0; mean = 0.09 [0.02,0.16], *E.E.* = 0.04, ***p.p.*= .98**, **$BF_{+0}$ = 48.79**). Additionally, interactions revealed substantial evidence that recurrent presentation of the same PE during fMRI compared to originals was retrieved with the same speed for Position 1 and 2 ($H_0$: *rep*:Pos2 = 0; mean = -0.01 [-0.13,0.11], *E.E.* = 0.06, *p.p.*= .88, **$BF_{01}$ = 7.64**). We also found substantial evidence that re-experience of varying PEs (vs. originals) during scanning led to the same recall speed of original objects in the memory test ($H_0$: *var*:Pos2 = 0; mean = 0.07 [-0.05,0.2], *E.E.* = 0.06, *p.p.*= .81, **$BF_{01}$ = 4.15**). Further, repeated experience of the same and varying PEs led to a similar object retrieval speed in Position 1 and 2 ($H_0$: *rep*:Pos2 – *var*:Pos2 = 0; mean = -0.08 [-0.21,0.04], *E.E.* = 0.0, *p.p.*= .83, $\boldsymbol{BF_{01}} = \mathbf{5.06}$).

### Familiarity and Vividness

First, we inspected familiarity ratings with regard to whether participants accurately identified an episode as known from the training session. We analyzed ratings using a non-parametric one-way rmANOVA with the factor MODIFICATION$_{\text{FMRI}}$ (*ori, var, rep*). We did not find a significant main effect of familiarity ($F(2, 72) = 0.28$, $p = .76$, $\eta^2p = .008$) indicating that participants were able to recognize an encoded episode as belonging to the training session. Regarding corresponding RTs on correct responses, a total of 7.02% of the trials were excluded as extreme outliers. The main effect did not reach significance ($F(2, 72) = 0.27$, $p = .76$, $\eta^2p = .007$).

Second, a non-parametric rmANOVA with the factor MODIFICATION$_{\text{FMRI}}$ (*ori, var, rep*) was conducted to analyze participants' vividness ratings and corresponding RTs on videos correctly assigned to the training session. We did not find a significant main effect of MODIFICATION$_{\text{FMRI}}$ ($F(2, 72) = 0.28$, $p = .76$, $\eta^2p = .01$) suggesting that episodes were equally vivid irrespective of prediction violation during scanning. For RTs related to the question of vividness, we found a trend for the main effect of MODIFICATION$_{\text{FMRI}}$ ($F(2, 72) = 2.68$, $p = .075$, $\eta^2p = .069$). Descriptively, participants showed fastest responses when presented with a repetitive PE ($M_{rep}$ = 2099 ms ± 83 ms) and slowest responses for varying PEs ($M_{var}$ = 2297 ms ± 88 ms).

## DISCUSSION

Episodic memories are prone to change, which helps to integrate new information into existing memories and thus maintain long-term valid assumptions and expectations. In the current fMRI study, we aimed to disentangle the neural networks underlying the re-experience of multiple and single alternatives competing with existing episodic memories. We triggered memory reactivation by presenting either multiple alternative versions of an originally encoded episode (varying PE), or only one single alternative version repeatedly (repetitive PE). While both conditions revealed brain activity that is typical for the detection of unexpected information in observed actions, we could identify distinct contributions of these and further areas to the processing of varying and repetitive changes. As expected, the BOLD results showed that both episodic PEs were associated with brain areas involved in memory reactivation and recognition of mismatches, but also elicited specific brain activity in each case. This difference was supported by substantial evidence at the behavioral level: In contrast to the experience of multiple alternatives, repeated exposure to the same alternative version of an episode enabled expectancy adaptation and potentially impeded subsequent recall of the original version. The results contribute to the distinction between the neural signatures of violation of episodic predictions and those of adaptation to episodic predictions.

## Brain responses to varying episodic prediction errors

PEs drive the updating of encoded memories while having the greatest impact during first encounter (Exton-McGuinness et al., 2015; Fernández et al., 2016). During varying PEs, participants never experienced an alternative version of an encoded episode twice in a row. As a result, there was no opportunity to correctly adjust predictions in response to continuous changes in content. Looking at the direct contrast between varying and repetitive alternatives, and at their conjunction, thus isolates the effect of PE, initializing the updating of episodic memory based on the amount of interference over time.

Starting with the conjunction of both conditions, episodic prediction errors were reflected in increased BOLD response in the hippocampus, which is related to episodic memory reactivation (Jeong et al., 2015), mismatch detection (Kumaran & Maguire, 2006), associative learning and generating predictions (Chen et al., 2011). Previous studies also found HC involvement in episodic prediction errors, though only subthreshold possibly due to less frequent PE repetitions (Jainta et al., 2022; Siestrup et al., 2022, 2023). In contrast to previous studies (Bein et al., 2020; Duncan et al., 2014), hippocampal subregions were not indicative of differentiating between varying and repetitive PEs in the present study (cf. Limitations). Remarkably, amygdala was co-activated with hippocampus. Studies in rodents and humans suggest that the amygdala modulates memory consolidation and plasticity processes in the hippocampus (Roesler et al., 2021). This modulation has been mostly investigated in the context of highly relevant, i.e., emotionally loaded or stressful contexts (Phelps, 2004; Roozendaal et al., 2009). In the present study, we did not use emotionally valanced stimuli but videos showing episodes that included typical everyday actions (e.g. relaxing at the pool) or fictional settings (e.g. knights at a tavern). We speculate that the amygdala modulated hippocampal-mediated responses to induced PE since these were accompanied by some increased arousal, that is, a small but consistent stress response. Note also that the amygdala was also reported for declarative memory recall of emotionally neutral objects (Inman et al., 2018).

Hippocampal and amygdala activity was accompanied by engagement of the ventrolateral prefrontal cortex, an area that is most reliably involved in expectation-violating information in observed actions (El-Sourani et al., 2019; Schiffer & Schubotz, 2011; Siestrup et al., 2022; Wurm & Schubotz, 2012). Similarly, posterior parietal regions (SPL, IPS) have been reported for PE highlighting the discrimination of original memories and alternative episodes (Cabeza et al., 2011; Ciaramelli et al., 2008; Uncapher & Wagner, 2009), especially also in the context of remembering the positions of objects in space (Harrison et al., 2010). These regions and, most prominently, the bilateral fusiform gyrus, were even more engaged for varying than for repeated single episode manipulations. Therefore, they most likely reflect the dissimilarity of multiple episodic PEs, as compared to always having the same expectation violation in the *rep* condition. In our experiment, this dissimilarity existed at the level of object information, the processing of which is related to superior parietal (Uncapher & Wagner, 2009) and fusiform (Weiner & Zilles, 2016) areas. Varying PEs moreover engaged caudate nucleus significantly more than originals, and also compared to repeated single PE when corrected with an FDR of 0.05. Caudate has been reported for signaling PE in different types of non-reward based learning paradigms (Badgaiyan et al., 2007; Den Ouden et al., 2010; Schiffer & Schubotz, 2011). Hence, persistent caudate activity may highlight an unstable state in which learning the latest version (here: exchanged object) does not increase predictive success.

Interestingly, the here-found brain network including HC, amygdala, and caudate, has been associated with reflecting the experience of 'unexpected uncertainty' during sequential learning (Soltani & Izquierdo, 2019; Yu & Dayan, 2005). Unexpected uncertainty refers to the encounter of unexpected changes in the environment, i.e. a variation of unpredictable mismatches between predictions and perceptual input. In contrast, expected uncertainty reflects the level of predictable changes arising from revised predictions regarding prior knowledge. Presenting participants with varying versions may have led to recurrent unexpected uncertainty during cued episodic memory retrieval. Thus, recurrent violation of top-down predictions was in conflict with prediction adaption. While expected uncertainty is suggested to enhance subsequent learning, random variation under constant probabilities does not (Courville et al., 2006). Here, we argue that unpredictable changes prevented episodic memory updating in a way that the original episode was still accessible during subsequent memory testing.

## Learning from repeated same episodic prediction errors

To investigate the effects of updating episodic predictions through repetitive PEs, we analyzed recurrent experience of single alternative versions in contrast to varying versions and to originals. It is suggested that new information presented at episodic memory retrieval allows for incorporation of new information over time as an adaptive learning process (Lee et al., 2017). We found substantial evidence that originally encoded objects were recalled less accurate after being presented with a repetitive PE. In contrast, although varying PEs yielded strong and distinct brain responses, they did not result in interference strong enough to hamper subsequent recall of the original episode. Experiencing multiple alternative episodes rather may have facilitated change monitoring, maintaining the initial memory and leading to retrieval performance comparable with originals. For the *rep* condition, however, an alternative version of the episode could be learned after repeated presentation and later led to a reduction in recall performance in the memory of the original episode, possibly due to competition. These findings support the view that memory strength of the newly established memory trace seems to be a crucial boundary condition for memory updating (Fernández et al., 2016).

The substantial evidence for the behavioral effect of repeating PEs compared to varying PEs was reflected at the brain level. Thus, the repetitive vs. varying PEs contrast showed largely the same activation pattern as the contrast between original and novel videos. In accordance with our previous study (Jainta et al., 2022; Siestrup & Schubotz, 2023), activity in cortical midline structures including the pgACC and the pmCC as well as in somatosensory and insula areas signaled successful retrieval of encoded episodic compared to novel information (Konishi et al., 2000). This network suggests that due to repeated presentations of the same modified episodes, subjects integrated a new episode variant into their internal model.

Considering a recent meta-analysis (Palomero-Gallagher et al., 2019), the here-found pgACC area is functionally connected to mCC and pCC (Palomero-Gallagher et al., 2019). Via connections to parietal cortex and HC, pCC was suggested to contribute to action-outcome learning (Rolls, 2019) and self-referential processing (Northoff et al., 2006). The here found co-activation of pgACC and pCC highlights the observation that pgACC's activity is triggered by matching similar experiences and/or challenging well-learned episodes with new, but similar information. In previous studies, we consistently found pgACC when contrasting originally encoded with new episodic information (Jainta et al., 2022; Siestrup et al., 2023). Of particular interest to our findings is that in a previous study (Siestrup & Schubotz, 2023), pgACC activation was increased in response to episodic modification in a PE condition characterized by strong memory modification effects in the post-fMRI memory test. Notably, in our other study (Siestrup et al., 2022) pgACC, mCC, pCC and hippocampal activity increased over time for later false memories, pointing to a process related to new memory encoding. While in the present study, we did not test memory on modified versions and hence, false alarms could not be examined, we did find a decreased recall of episodes that were presented repeatedly modified during the fMRI session. Furthermore, when two slightly diverging episodes had been encoded, pgACC was found to be more activated for biased vs. balanced episodic expectations (Schiffer et al., 2013). Together, these findings fit very well to the proposed pgACC's role in deciding for one option over others (Klein-Flügge et al., 2022). We therefore conclude that in the present study, pgACC together with mCC and pCC reflect that in case of repetitive as in contrast to varying PE, robust second, alternative versions of the corresponding original episodes were established. With this in mind, it seems particularly interesting to further investigate the role of pgACC in episodic memory plasticity in future studies.

## LIMITATIONS

We explored distinct contributions of hippocampal subregions CA1 and CA3. Despite the significant BOLD response in HC during experience of PEs, activity in hippocampal subfields did not differ between repetitive and varying PEs during memory retrieval. This contrasts with previous findings suggesting increased CA1 activity during predictive success and decreased CA1 activity during experience of multiple PEs at a time compared to CA3 (Bein et al., 2020). As we did not replicate this activity pattern, we assume that hippocampal subfield activity may be indicative of the amount of experienced interference at a time rather than over time. Further, discrepancies in PE-related brain activity may further arise from different types of employed PEs, i.e. interrupting episodic retrieval (Sinclair et al., 2021) or using static (Bein et al., 2020) or dynamic sceneries with almost identical content (Jainta et al., 2022; Siestrup et al., 2023). Further research is needed to understand the complexity of hippocampal responses to PEs.

As a caveat, we did not show direct evidence of brain-behavior interaction in the current study. While we focused on investigating the neural differences during experience of repetitive and varying PEs, we acknowledge the limitation of not directly linking these neural findings to behavioral outcomes. This highlights the need to directly demonstrate the interaction between brain activity patterns and behavioral outcomes in future studies.

Also, future studies should test whether balancing the number of presentations of each episode regarding repetitive and varying PEs, i.e. presenting each varying version eight times, will lead to stronger impairment of memory performance after recurrent experience of varying versions. It is possible that potential effects of varying PEs on subsequent memory retrieval may depend on the encoding strength of alternative information. Therefore, this approach could shed further light on how potential boundary conditions could affect the updating of episodic memory through prediction errors.

## CONCLUSION

Our study sheds light on the shared and distinct effects of varying and repetitive mnemonic prediction errors during episodic memory retrieval. Whether through varying or repetitive prediction errors, hippocampus and amygdala, along with a number of neocortical areas, were involved in processing new information that occurred during episodic retrieval. This new information was linked to the originally encoded episode only if this prediction error was repeated in an identical way. In this case, our findings extend the role of cortical midline activity beyond mismatch monitoring in episodic memory to possibly having an impact on expectation adaptation through episodic memory reactivation. Further research is needed to understand the multifaceted functions of cortical midline activity in episodic memory reactivation and updating.

### Data Availability Statement

The data sets generated for this study are available on request to the corresponding author.

### Author Contributions

**Benjamin Jainta:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – Original Draft Preparation, Writing – Review & Editing, Visualization

**Ricarda I. Schubotz**: Conceptualization, Methodology, Resources, Writing – Original Draft Preparation, Writing – Review & Editing, Supervision, Funding acquisition

**Dr. Anoushiravan Zahedi**: Formal analysis, Writing – Review & Editing.

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### Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. In the current paper, we report its proportions of citations (successfully categorized DOIs = .797) by gender category to be as follows: M/M = .34; W/M = .234; M/W = .234; W/W = .204.

### Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

### Ethics Statement

This study involving human participants was reviewed and approved by the Ethics Committee of the Department of Psychology, University of Münster. Participants signed an informed consent before participation.

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# 4 General Discussion and Future Directions

Episodic memories are prone to change and do not always reflect faithful representations of personally experienced events. This seemingly imperfect system perfectly fits in a dynamic world that requires memory updating to provide predictive success. There is much evidence that PEs can trigger an updating process leading to memory modification, i.e., strengthening, weakening, or altering information stored in the system. Therefore, when expectations are not aligned with reality, the need to update drives the encoding of relevant new information. The present work aimed to investigate the neural substrates and modulating factors of mnemonic PEs and their impact on episodic memory modification.

## 4.1 Summary of the Presented Studies

**Study 1** (Jainta et al., 2022) aimed to investigate how self-referential factors, i.e., agency and perspective, modulate the neural substrates of mnemonic PEs and their impact on episodic memory outcomes. Participants encoded episodes showing toy stories from demo videos by either imitating or actively observing an actress. In the subsequent fMRI session one week later, participants were either presented with videos showing episodes in their original or a slightly modified version. Modifications either affected the content (i.e., change of an object) or the structure (i.e., change of two adjacent action steps) of an episode as described in a companion paper (Siestrup et al., 2022). After scanning, participants completed a post-fMRI memory test during which they were presented with both original and modified versions of an encoded episode. Presenting subjects with videos of encoded or slightly modified episodes triggered increased activity in posterior and anterior cingulate cortex, precuneus, midfrontal gyrus and insula, suggesting successful episodic retrieval (Jeong et al., 2015; Rugg & Vilberg, 2013). In contrast to originals, modified episodes engaged brain areas typical for processing PEs, involving ventrolateral prefrontal and parietal cortices (unpublished data from **Study 1**). While retrieval perspective led to substantial brain responses for completely new episodes, these effects were nearly eliminated for encoded episodes. Interestingly, when participants were only observing, but not performing, actions during encoding, cued retrieval through modified episodes triggered significantly weaker activation in the hippocampus. However, this effect did not translate to behavioral performance in the subsequent fMRI memory test. In general, when presented with a modified episode in the scanner, this modified version was more often later mistaken as originally encoded. Accordingly, modified episodes led to falsely considering originals as not previously encoded, particularly when presented from a 3pp. Taken together, the overall effect of mnemonic PE was strong in brain and behavior, whereas the impact of self-referential factors on PE and subsequent memory performance was rather subtle.

**Study 2** (Siestrup et al., 2023) focused on the impact of memory solidity on the neural processing of cued episodic retrieval concerning mnemonic PEs. First, subjects encoded episodes by imitating episodes presented from 1pp. To further consolidate episodic memories, participants actively retrieved encoded stories in two pre-fMRI retrieval sessions, taking place one day and one week after encoding. To this end, participants re-encountered each episode either twice or eight times, following a spaced (retrieval during both sessions) or a massed fashion (retrieval during the second session). Both fMRI and the subsequent memory test were conducted as described as in **Study 1**. Presenting subjects with modified episodes reactivated brain regions of the episodic memory network. Moreover, substantial brain responses were found in hippocampus and ACC for modified episodes, when resulting in false memories during subsequent testing. Further, modified episodes increased frontal activity, specifically the ACC, when episodes were retrieved more often during pre-fMRI sessions. Retrieval occurring in a spaced rather than a massed fashion elicited brain responses across the episodic memory network, including pCC, precuneus, and superior parietal lobe

(SPL). While retrieving episodes more (than less) frequently led to better memory performance for originally encoded episodes, there was no benefit resulting from a history of spaced versus massed retrieval. In summary, **Study 2** provided evidence for hippocampal and cortical involvement in dynamic learning through PEs leading to false memories. Additionally, **Study 2** highlighted the influence of retrieval protocols on brain responses to mnemonic PEs as well as subsequent memory retrieval.

In **Study 3** (Jainta et al., 2024), the focus was on characterizing brain responses underlying the experience of varying and repetitive PEs and their impact on object recall from originally encoded episodes. To this end, participants encoded episodes by actively observing demo videos. A day after encoding, subjects returned for the fMRI session. During scanning, participants experienced original or slightly modified versions of an encoded episode. For modification, either multiple, ever-changing versions (varying) or a single alternative version (repetitive) were presented repeatedly. On day three, participants conducted a post-fMRI memory test in which episodic memory retrieval was triggered, and object recall was tested for originally encoded objects from day one. Both repetitive and varying modifications triggered increased brain activity in the hippocampus, amygdala, SPL, inferior parietal sulcus (IPS), and vlPFC, areas typically observed in mismatch detection. Further, distinct neural signatures were identified for each modification type. For instance, varying PEs (compared to repetitive PEs) led to stronger blood-oxygen level-dependent (BOLD) responses in the hippocampus, SPL, and bilateral fusiform gyrus, indicating the experience of dissimilarity between multiple alternatives. In addition, varying PEs involved activation of the caudate nucleus, reflecting a state of uncertainty in learning. In contrast, recurrent encounters of repetitive (vs. varying) PEs resulted in increased brain activity of cortical midline structures, like the ACC and posterior mid-cingulate cortex, as well as somatosensory and insular cortices, suggesting the integration of relevant new information into an existing internal model. This finding was corroborated by behavioral results, indicating that repetitive (but not varying) PEs impaired later recall of originally encoded objects. Together, findings highlight shared and distinct effects of varying and repetitive PEs when experiencing mnemonic PEs during cued episodic retrieval.

## 4.2 Prediction Errors – A Driving Force Behind Learning

Our brains are constantly engaged in the process of generating expectations to successfully predict the future (Clark, 2013, 2015; Friston, 2003). When expectations fail, a PE signals a mismatch between predicted and current experience to update an internal model of the world (Friston, 2003, 2005). PE signals are reflected by an increased activation in specific brain regions (e.g., D'Astolfo & Rief, 2017; den Ouden et al., 2012; Wang et al., 2017). Of note, PEs are not only surprise responses to perceptual mismatches but are closely linked to higher-order representations (den Ouden et al., 2012). Although episodic memory was characterized by its function of predicting the future based on the personal past, research regarding learning from PEs in episodic memory appears to be still in its infancy. In general, memory modification during episodic retrieval was suggested to be strongly driven by PEs (Fernández et al., 2016; Kim et al., 2014; Sinclair & Barense, 2019), raising the question of how different types of mnemonic PEs affect neural substrates of episodic memory and subsequent memory performance. To target this question, we adapted an episode modification paradigm for **Studies 1**, **2**, and **3** (Schiffer et al., 2012, 2013) where episodes with (varying) encoding histories were first established and then violated regarding their content.

### 4.2.1 Neural Substrates Underlying Mnemonic Prediction Errors

PE signaling was demonstrated to be a widely generalized mechanism involved in associative, social, and reinforcement learning (e.g., Gershman & Daw, 2017; Holland & Schiffino, 2016; Joiner et al., 2017). Investigating the different neural correlates underlying

PEs is crucial when examining the effects of PEs on memory modification. For instance, previous research showed PEs to trigger increased brain activation in prefrontal, hippocampal, parietal, and striatal areas (Bein et al., 2020; D'Astolfo & Rief, 2017; Schiffer et al., 2012; Schiffer & Schubotz, 2011; Wang et al., 2017). By applying an episode modification paradigm in **Studies 1**, **2**, and **3**, we cued memory retrieval using original and modified versions of an episode. Therefore, we expected to see activation of brain regions involved in mismatch detection as well as episodic memory retrieval.

In our studies, we repeatedly found enhanced neural responses to mnemonic PEs in vlPFC, including inferior frontal sulcus (IFS) and inferior frontal gyrus (IFG), i.e., Brodmann area (BA) 44 and 45. Our findings align with previous research demonstrating the vlPFC to facilitate the selection between competitively activated mnemonic representations (Badre et al., 2005; Moss et al., 2005; Schlichting et al., 2015) and detection of highly informative or inconsistent contextual details in action observation (El-Sourani et al., 2019; Hrkać et al., 2015; Wurm & Schubotz, 2012). Specifically, BA 45 of the IFG was suggested to be involved during encoding (Kuhl et al., 2012) and top-down retrieval control of relevant information (Wimber et al., 2015). In general, lateral PFC contributes to generating experience-based predictions (den Ouden et al., 2012; Schubotz, 2015) and regulation of memory reactivation as well as memory updating (Kluen et al., 2019; Kuhl et al., 2012). In the above-mentioned studies, vlPFC activation was predominantly found in the left hemisphere (Badre et al., 2005; Kluen et al., 2019; Kuhl et al., 2012; Moss et al., 2005; but see Schlichting et al., 2015, for bilateral activation). However, **Studies 1** and **2** revealed stronger engagement of the right vlPFC during repeated experience of PEs. According to the HERA model by Habib et al. (2003), increased activity of the left PFC is associated with encoding, whereas stronger activation of the right PFC is associated with retrieval. In line with this proposal, activity in the right vlPFC in our studies may be indicative of retrieval rather than encoding-related processes.

Moreover, cued retrieval of modified episodes engaged brain regions that were repeatedly found to be involved in the processing of mnemonic PEs (**Studies 1**, **2**, and **3**; for additional replications, see Siestrup et al., 2022; Siestrup & Schubotz, 2023). Specifically, these were IPS/SPL, precuneus, and fusiform gyrus. The observed activation of IPS in our studies aligns with previous research linking activation of IPS to action observation (Richter et al., 2019) and successful episodic retrieval (Wagner et al., 2005). Further, the SPL was suggested to regulate top-down attention supporting retrieval monitoring (Cabeza et al., 2008; Hutchinson et al., 2014) and allocating attention toward new or unexpected information (Molenberghs et al., 2007; Tamber-Rosenau et al., 2011). Additionally, the superior parietal cortex was proposed to reflect greater demands for attention regulation during retrieval in the context of uncertainty (Hutchinson et al., 2014). This becomes particularly crucial in scenarios where additional post-retrieval processes need to discriminate between stored and new information (Cabeza et al., 2011; Ciaramelli et al., 2008). Accordingly, our results indicate the involvement of superior parietal areas in processing PEs during episodic retrieval. Due to its role in the encoding of episodic memories (Uncapher & Wagner, 2009), superior parietal cortex potentially contributes to memory updating from PEs.

Embedding our study results into the larger body of literature, mnemonic PEs triggered activation of ventrolateral prefrontal and superior parietal areas, highlighting their role in processing mismatches during episodic retrieval.

### *Hippocampal Contributions*

The hippocampus is proposed to play a crucial role in generating predictions and detecting associative mismatches between internal models and current perception (Chen et al., 2011; Duncan et al., 2009; Kumaran & Maguire, 2007; Long et al., 2016). As the hippocampus has been suggested to be a core structure of episodic memory sharing common functions with the PFC during encoding and retrieval (Rugg et al., 2015), we expected enhanced hippocampal responses to mnemonic PEs during episodic retrieval.

Despite the widely recognized role of the hippocampus as a mismatch detector (e.g., Duncan et al., 2012; Kumaran & Maguire, 2007), our results were rather mixed across studies. During the experience of mnemonic PEs, we observed a mean deactivation of the hippocampus in **Study 1** when participants encoded episodes by only observing compared to self-performing, especially in the left hemisphere. We interpreted reduced hippocampal activity indicative of a decreased sensitivity to detect mnemonic PEs, possibly stemming from a lower level of detail in self-encoded information in the observation condition (Rabin et al., 2010). Interestingly, **Study 2** revealed weaker hippocampal responses for modified compared to original episodes following the spaced retrieval practice. Aside from its role in mismatch detection, previous research indicated the hippocampus to be selectively activated to support encoding of overlapping events (Schlichting & Preston, 2016) and recollection of associations (Davachi & Wagner, 2002; Giovanello et al., 2004). For instance, hippocampal activity was found to increase with matching and decrease with mismatching information for previously encoded word pairs (Giovanello et al., 2004). In **Study 2**, cued retrieval of modified, in contrast to original, episodes may have generated weaker recollection of its prior occurrence and, therefore, resulted in a mean deactivation of the hippocampus. Moreover, stronger engagement of the hippocampus during exposure to originals may reflect the reinstatement of encoded episodes (Giovanello et al., 2004).

Albeit at a subthreshold level, **Studies 1** and **2** identified the involvement of hippocampus in PE signaling. In **Study 3**, whole-brain analysis revealed both repetitive and varying PEs to trigger enhanced hippocampal activity, potentially resulting from more frequent PE repetitions compared to **Studies 1** and **2**. However, explorative region of interest (ROI) analysis of hippocampal subfields did not differ between repetitive and varying PEs during memory retrieval, contrasting previous findings (Bein et al., 2020; Duncan et al., 2014). Of note, other studies did not replicate the effects of mismatch detection for hippocampal regions (D'Astolfo & Rief, 2017; Sinclair et al., 2021), axis (Siestrup & Schubotz, 2023), or hemisphere (Sinclair et al., 2021).

In summary, mixed findings raise the question of what reminding procedures as well as which conditions affect hippocampal signatures of memory modification and reinstatement in response to mnemonic PEs.

### 4.2.2 Neural Responses to Different Types of Mnemonic Prediction Errors

Previous studies found internal model updating through PEs to depend on the model's solidity and, thus, to occur slower for strong and faster for weak internal models (e.g., Schiffer et al., 2013). Schiffer et al. (2013) argued that internal models must be updated when predictions are in conflict with real-world experience. Nevertheless, they emphasized the importance of avoiding unwarranted revisions to maintain the predictive benefits of previous experience. For this reason, we investigated how different types of PEs (i.e., varying and repetitive alternatives) interact with original memories.

In **Study 3**, we aimed to identify common and distinct neural responses to varying and repetitive PEs. Therefore, we expected both types of PE to trigger brain responses in regions typical for mismatch detection. Moreover, we hypothesized the commonly shared regions to be more enhanced during exposure to varying PEs, while repetitive PEs were expected to trigger brain activation in areas associated with episodic retrieval. In fact, both varying and repetitive PEs led to increased brain activity in vlPFC, PPC, and hippocampus, regions typical for mismatch detection (D'Astolfo & Rief, 2017; Duncan et al., 2012; Kumaran & Maguire, 2007; Wang et al., 2017). As expected, this network was stronger engaged during the experience of varying (vs. repetitive) alternatives due to the repeatedly refreshed PE. Interestingly, comparing varying PEs to original episodes revealed increased activity in the caudate nucleus, hippocampus, and amygdala. The caudate nucleus has previously been identified during the experience of perceptual PEs (Schiffer & Schubotz, 2011). Further, activity in caudate nucleus was demonstrated to decrease during learning of new contingencies (e.g., Delgado et al., 2005; Ruge & Wolfensteller, 2010) suggesting a role in storing gradual accumulation of alternative versions. These findings are in line with our interpretation that increased activity in caudate nucleus may indicate an unstable cognitive state wherein learning the latest version of an episode does not lead to improved predictive success. Together with amygdala and hippocampus, caudate nucleus is part of a brain network involved in experiencing unexpected uncertainty, a state in which internal models deal with unpredictable mismatches that do not enhance learning. In line with the above-mentioned proposal from Schiffer et al. (2013), non-predictable changes in an episode may have prevented internal model updating, leaving original memory traces retrievable during later memory testing. This assumption is further supported by behavioral evidence from the post-fMRI memory test (cf. section 4.2.3).

In contrast, the experience of repetitive (vs. varying) PEs in **Study 3** evoked distinct patterns of brain activity in ACC, pCC, and insula. These areas are part of a network previously found during successful episodic recall (Rugg et al., 2015). In studies of our own group, ACC and pCC were repeatedly found when comparing originally encoded with completely new episodes (**Study 1**; **Study 3**; Siestrup et al., 2022; Siestrup & Schubotz, 2023). However, these areas were not only identified to contribute to retrieval. Especially the ACC was demonstrated to be involved in learning from PEs (Rushworth et al., 2011; Vassena et al., 2017) and conflict monitoring (Botvinick et al., 2004; Vassena et al., 2017). More importantly, activity in ACC and pCC was found to gradually increase for modified episodes over time when resulting in false memory formation (**Study 2**). Therefore, we suggest this activation during the experience of repetitive, but not varying, alternative episodes to be indicative of integrating this episodic version into their internal model and subsequently competing with originals during memory recall.

In summary, we delivered first evidence for our third research question, namely how do different types of mnemonic PEs affect neural responses underlying learning from PEs in episodic memory. To this end, we were able to show that experiencing varying and repetitive PEs share a common neural ground, but further recruit distinct brain responses respectively. Distinct neural signatures provide evidence for internal model updating in case of repetitive, but not varying PEs. However, while differences in neuronal responses to different types of PEs exist, future research needs to investigate under what conditions varying and repetitive PEs may further interfere with original memories, especially during subsequent testing.

### 4.2.3 Behavioral Findings

Mnemonic PEs were suggested to cause memory destabilization to allow subsequent reconsolidation and memory modification (Exton-McGuinness et al., 2015; Fernández et al., 2016). Behavioral evidence supports but also challenges the idea of memory modification through PEs. While some studies have shown that PEs can alter episodic memories (Sinclair et al., 2021; Sinclair & Barense, 2018), others highlighted boundary conditions of (Quent et al., 2022; Wahlheim & Zacks, 2019) or even failed to support this notion (Hermann et al., 2021). Therefore, the full spectrum of memory modification through PEs remains to be demonstrated.

In studies of our own group, we repeatedly found that recurrent exposure to modified episodes led participants to erroneously accept those modified versions as originally encoded (**Studies 1** and **2**; also see Siestrup et al., 2022 and Siestrup & Schubotz, 2023 for further evidence). Interestingly, modified episodes did not confuse episodic memory for originally encoded episodes, i.e., high correct acceptance rates for originals. It remains unclear how exactly mnemonic PEs affected episodic memories. Previous studies suggested that memory modification may arise from interference between old and new memory traces (Klingmüller et al., 2017; Sinclair & Barense, 2018, 2019) or from source confusion (Hekkanen & McEvoy, 2002). In **Studies 1** and **2**, participants were repeatedly presented with novel episodes, i.e., episodes which have not been part of the set of originally encoded episodes. Despite recurrent presentation with novel episodes during fMRI, participants correctly recognized novel episodes as not previously encoded. Therefore, source attribution may not explain results from **Studies 1** and **2**. Both **Studies 1** and **2** demonstrated high correct acceptance rates for original episodes after experiencing modifications in the scanner. Together, these findings suggest that original memory traces remained largely unimpaired, while additional information was integrated into an existing model. This interpretation aligns with previous research indicating that the integration of new information does not necessarily result in less accurate retrieval of original episodes (Elsey et al., 2018; Sinclair & Barense, 2018; St. Jacques, Olm, et al., 2013). Although some researchers proposed that original memory traces may be overwritten with new content (Elsey et al., 2018; Richards & Frankland, 2017), contrasting evidence suggested recollection of the initial memory to be only weakened, rather than replaced (Kim et al., 2014).

In **Study 3**, we were interested in whether modified episodes would hamper cued recall of original objects during later recall. Although repeated retrieval of the same modified episode led to less accurate object recall, we did not find evidence that participants replaced original objects with those violating expectations (unpublished data). In the case of varying modified episodes, recall of original objects remained largely intact. We interpreted our behavioral results in favor of the notion that memory strength of newly acquired information may play a critical boundary condition for memory modification (Fernández et al., 2016).

Additionally, it was demonstrated that distinct information that deviates from the current context may be beneficial for original memory performance (Hunt, 2013; Sommer & Sander, 2022). For this reason, the experience of varying PEs may have contributed to the distinctiveness between original and modified episodes as multiple object modifications potentially facilitated change monitoring. Hence, multiple alternative episodes did not compete sufficiently with the recall of original objects. This behavioral pattern is in line with a recent proposal by Bein et al. (2021), arguing that the necessity of remembering an alternative event depends on the frequency of occurrence. When an alternative event has been experienced only once in a particular way, it may not be essential to remember this version as the original memory may provide long-term predictive success. Conversely, if an alternative event has been experienced multiple times in the same way, it may be beneficial to remember this version to increase predictive success for future occurrences thereof. Despite finding less accurate recall of original objects after repetitive (but not varying) PEs in **Study 3**, it remains unclear whether false memories were created as we did not test memory on modified versions. Nonetheless, these findings may offer a promising starting point to broaden our understanding of learning from different types of PEs.

Taken together, our research findings provide support for memory modification based on the experience of PEs, i.e., maintaining the original and encoding a modified episode. With respect to **Studies 1** and **2**, it is plausible to suggest that two distinct alternatives of an episode were encoded and integrated into the internal model. Further, **Study 3** highlighted that the repeated experience of the same alternative stands more likely in conflict with an originally encoded memory than exposure to multiple different versions.

## 4.3 Conditions Rendering Episodic Memory

A central yet unresolved question is which conditions render a more or less stable episodic memory of our personal past. To better understand the conditions and mechanisms underlying episodic memory, the current thesis aimed to investigate potential factors affecting the encoding, consolidation, and retrieval.

### 4.3.1 The Self in Episodic Memory

Episodic memory is characterized by autonoetic consciousness or the awareness that one has been part of the recalled event, i.e., the subjective experience of self in time (Gardiner, 2001). Regarding difficulties in experimental operationalization, as well as mixed findings, there is an ongoing debate about whether autonoetic consciousness is critical for episodic memory (Cheng et al., 2016; Cheng & Werning, 2016; Henke, 2010; Klein, 2016). Irrespective of whether autonoetic consciousness is considered a fundamental aspect or simply a byproduct of episodic retrieval, research findings from both behavioral and neurophysiological studies indicate that self-referential factors, namely the agentive state (cf. section 1.3.2) and visual perspective (cf. section 1.3.1), play important roles in episodic memory retrieval.

#### *The Role of Agency*

Several studies have suggested that performing rather than passively experiencing (e.g., observing) an action results in more accurate memory retrieval (e.g., Hornstein & Mulligan, 2001; Mulligan & Hornstein, 2003; Senkfor et al., 2002). The advantage of performing an action, or the so-called enactment effect (Roberts et al., 2022), was found to be reflected by increased activation of parietal and motor cortices, as well as SMG (Krönke et al., 2013; Leynes et al., 2005, 2006; Nyberg et al., 2001; Senkfor et al., 2002). However, the enactment effect was only investigated in paradigms using very simple actions (see Roberts et al., 2022).

On a neural basis, **Study 1** identified marginal effects of self-performance during encoding for later retrieval. Interestingly, this was only the case for cued retrieval using modified, but not original, episodes. For formerly performed rather than solely observed episodes, modification triggered increased activation of the medial frontal cortex (MFC) in BA 10, and posterior precuneus. Further, a history of encoding through mere observation versus self-performance resulted in decreased hippocampal activity during cued retrieval of modified episodes. The hippocampus contributes to generating predictions and detecting associative mismatches (Chen et al., 2011; Duncan et al., 2009; Kumaran & Maguire, 2006). Therefore, stronger activity for previously self-performed actions may reflect a higher sensitivity in response to expectation violation. This is in line with the activation of MFC reflecting the generation of internal states and monitoring of episodic success (Ramnani & Owen, 2004). Moreover, recent research suggests this region to be indicative of internal model solidity and contributes to mismatch detection between expected and relevant new information (Schiffer et al., 2012, 2013). Therefore, self-performed actions may have resulted in stronger predictions than those derived from observed actions.

However, agentive states were ineffective on the behavioral level following the recurrent experience of mnemonic PEs during fMRI. This finding is in strong contrast to previous research suggesting enactment benefits for episodes in which participants actively performed, not solely observed actions (e.g., Hornstein & Mulligan, 2001; Mulligan & Hornstein, 2003). In **Study 1**, the complex multi-step episodes strongly differed from simple single-step actions used in previous studies. Moreover, intensive training using multiple presentations of demo videos during observation trials may have eliminated the benefit of enactment. Observing someone else perform an action that shares perceptual features with an action one has performed, may have resulted in the formation of motor representations for observed episodes, a phenomenon referred to as *observation inflation* (Lindner et al., 2010, 2016).

Despite decades of research, the mechanisms underlying the enactment effect are still under debate. On the one hand, it has been suggested that distinct sensorimotor features of an action enhance memory by enriching a memory trace with item-specific information during encoding which later may function as retrieval cues (Engelkamp, 2001). On the other hand, it has been argued that enactment effects result from cognitive rather than motor capacities involving the self and goals of the self (Kormi-Nouri, 1995). However, episodic memory was suggested to depend on successful binding and recollection of features from an original event, i.e., information about the *what, where,* and *when* (Tulving, 2002). Performing an action is inherently tied to interacting with the environment. Thus, integrating the content (what happened) within the spatial (where) and temporal (when) context of self-performed actions may offer a promising avenue for future research. One possibility to investigate complex, naturalistic episodes in a standardized manner may be the use of virtual reality, as it has been suggested in clinical settings (Schultheis et al., 2002). For instance, active navigation within virtual environments may provide a form of enactment effect potentially facilitating spatial and episodic memory (see, Tuena et al., 2019 for a review).

### *The Role of Visual Perspective*

It has previously been demonstrated that the perception of actions from 1pp compared to 3pp, and vice versa, activate fundamentally different brain networks (e.g., Wurm et al., 2011). Episodic memory retrieval does not necessarily depend on the visual perspective an episode was originally encoded from (e.g., Nigro & Neisser, 1983; Rice & Rubin, 2009). As we experience the world through our own eyes, it was suggested that an observer perspective during retrieval may be indicative of memory modification (Akhtar et al., 2017) or even reflect a false memory (Sutin & Robins, 2008). Therefore, the role of perspective in episodic memory and its underlying brain networks during retrieval are of particular interest.

**Study 1** revealed stronger BOLD responses for 1pp compared to 3pp in the supplementary motor area, anterior precuneus, postcentral gyrus, and areas belonging to the action observation network during the experience of completely new episodes. In contrast, during the experience of previously encoded episodes, this strong effect of visual perspective disappeared. Understanding the origin of 1pp and 3pp memories is essential to determine the factors that contribute to adopting a specific perspective during retrieval and potentially indicating memory distortions or inaccurate recollection. In **Study 1**, participants encountered each episode from both perspectives during encoding to counterbalance the different perspective experiences of self-performance and mere observation. Thus, subjects potentially stored episodic memories in a way in which retrieval perspective was not crucial or allowed adopting both perspectives for reconstructing the episode. This explanation is in line with a recent proposal, suggesting that even when experiencing a self-perspective during encoding an observer-like perspective may be stored due to constructive processes in memory (McCarroll, 2017). Therefore, this flexibility of perspective during remembering raises the question of which neural substrates reflect episodic retrieval perspective.

Neuroimaging studies reported larger precuneus volume in individuals retrieving autobiographical memories more frequently from 1pp than 3pp (Freton et al., 2014; Hebscher et al., 2018). Additionally, a recent fMRI study demonstrated that both 1pp and 3pp engage hippocampus, anterior and posterior midline, lateral frontal, and posterior cortices. In particular, adopting a 1pp was associated with stronger connectivity within MTL and ventromedial PFC during retrieval, while stronger hippocampal connectivity with posterior medial areas was identified for a 3pp (Iriye & St. Jacques, 2020). Further, it was reported that hippocampal activity is decreased when retrieving memories from an observer and increased during recall from a 1pp (Bergouignan et al., 2014; St. Jacques, Kragel, et al., 2013). Contrary to these findings, we did not find perspective to influence hippocampal or parietal activity in **Study 1**. The discrepancy between the above-mentioned research and our findings may result from a variety of differences between paradigms. For instance, Iriye and St. Jacques (2020) instructed participants to visualize the spatial location and content of a specific autobiographical memory either from 1pp or 3pp, leading to stronger engagement of imaginary and constructive processes than cued retrieval. In contrast, Bergouignan et al. (2014) used head-mounted displays and cameras to initiate encoding of 1pp or 3pp during oral examination of life events. Therefore, the encoding perspective was creating an in-body or out-of-body experience, rather than a 1pp or 3pp. It is important to note that differential brain activity patterns for 1pp versus 3pp potentially depend on how the retrieval perspective was initialized. Previous memory research triggered perspectives using visual imagery (Grol et al., 2017) or instructions to spontaneously adopt one (Freton et al., 2014) or actively shift to another perspective (Eich et al., 2009; St. Jacques et al., 2017) during free recall of autobiographical memories.

While only a hand full of studies investigated neural mechanisms underlying episodic retrieval perspective, most findings on effects of perspective emerge from behavioral research (e.g., Akhtar et al., 2017; Butler et al., 2016; Janssen et al., 2011; Marcotti & St. Jacques, 2018; Rice & Rubin, 2009). In line with these studies, participants in **Study 1** less often falsely accepted modified episodes as previously encoded when the original counterpart was presented from 1pp (vs. 3pp) during fMRI. Some researchers suggested greater availability of visual information during retrieval from 1pp (Butler et al., 2016; Libby & Eibach, 2011) which can be ruled out as 1pp and 3pp contained identical visual information since episodic videos were only manipulated by a 180° rotation. The 1pp rather allowed participants to focus their attention more on specific features (Libby & Eibach, 2011), enabling them to more likely detect modifications.

The above-mentioned studies provide a preliminary understanding of how encoding and retrieval perspectives may influence episodic memory. While most findings demonstrate superior effects of 1pp stemming from behavioral research, future neuroimaging studies need to clarify which distinct brain networks result from 1pp versus 3pp and vice versa.

*Summary of Agency and Perspective Effects*

Taken together, **Study 1** delivered preliminary evidence for answering the first research question of the current thesis on how agency and perspective affect brain responses to mnemonic PEs and episodic memory modification. The results indicate that internal models drawn from episodic memories associated with self-generated versus solely observed actions may be stronger and more sensitive to alterations. While this higher sensitivity for mnemonic PEs was reflected in brain activation, memory performance was not influenced by the agentive state. A contrary observation was made for the effect of visual perspective. While perspective subconditions did not lead to differential brain activations during the experience of PEs, retrieving episodes from a 3pp resulted in more false memories. The results of **Study 1** are a first indication of the subtle effects of agency and perspective during the experience of mnemonic PEs and subsequent memory performance in episodic memory.

### 4.3.2 Consolidation through Retrieval Practice in Episodic Memory

Consolidation takes a major role in mediating memory solidity through sleep (Cheng & Werning, 2013), as well as active retrieval (Antony et al., 2017). Recurrent retrieval can enhance memory performance (Antony et al., 2017) and, further, protect memories from later modification (Elsey et al., 2018). This so-called *testing effect* was identified as a robust phenomenon in a wide variety of materials for declarative memory (for reviews, see

(Roediger & Butler, 2011; Roediger & Karpicke, 2006). Accordingly, improvements in memory performance are associated with higher rather than lower retrieval frequencies of information and spreading retrieval practice over several occasions (spaced) rather than a single occasion (massed) (e.g., Karpicke & Roediger, 2008; Lyle et al., 2020). Therefore, consolidation may not only affect memory solidity but further have an impact on PE signaling (Exton-McGuinness et al., 2015; Fernández et al., 2016; Schiffer et al., 2013).

To provide a better understanding of additional retrieval practice in episodic memory, **Study 2** examined the influence of different retrieval protocols on neural substrates and behavioral outcomes of mnemonic PEs. In two retrieval sessions, participants experienced additional episodic retrieval through different retrieval schedules (spaced vs. massed) and retrieval frequencies (two vs. eight times).

With respect to general retrieval schedule effects, **Study 2** demonstrated stronger BOLD responses for spaced versus massed retrieval in brain areas associated with episodic memory retrieval as identified in **Study 1**. However, there was no behavioral evidence for more solid memories due to retrieval schedule. Therefore, this finding may not serve as enough proof for the effectiveness of retrieval schedules on memory solidity. As discussed in **Study 2**, it may be fruitful to reexamine the study design to maximize the effects of retrieval schedule (cf. Dobson et al., 2017; Gerbier & Toppino, 2015). For instance, a higher number of distributed retrieval (Dobson et al., 2017) or testing sessions as well as the type of testing (Kang, 2016) may affect potential effects of different retrieval schedules. Of note, hippocampal engagement was descriptively stronger for the spaced compared to the massed condition during retrieval of originally encoded episodes.

More frequent pre-fMRI retrieval resulted in less effortful retrieval, indicated by a decrease in ACC activity. This finding aligns with previous research suggesting a decrease of ACC activity indicative of more consolidated memories (Long et al., 2016). Accordingly, less rather than more retrieval increased activity in ACC and MFC (BA 9 and 10) during the experience of mnemonic PE. Consistent with findings of **Study 1**, cortical midline activation in **Study 2** reflected episodic memory retrieval. Previous research suggested cortical midline areas, like the ACC, to be more engaged during the experience of PE (Malekshahi et al., 2016; Schiffer et al., 2013) and internal model updating (Schiffer et al., 2012, 2013). This is further corroborated by the behavioral results of **Study 2.** Memory for originally encoded episodes was better after retrieving episodes more frequently between encoding and testing. More frequent retrieval, i.e., more solid memories, prevented the incorporation of alternative episodes. Therefore, after less frequent retrieval, participants showed a tendency to falsely accept modified episodes as veridical.

On the contrary, increased brain activity following less frequent retrieval of modified episodes in ACC (**Study 2**) does not match previous findings, showing stronger brain responses for more consolidated episodes (Bosshardt, Degonda, et al., 2005; Takashima et al., 2006; Wiklund-Hörnqvist et al., 2021). However, the observed activity pattern may result from increased cognitive demands during retrieval attempts after a longer consolidation period (e.g., Bosshardt et al., 2005). In **Study 2**, we considered less robust memories to potentially trigger more pronounced PE signaling as weaker internal models may have been more susceptible to relevant new information (e.g., Schiffer et al., 2013). Although retrieval frequency affected subsequent memory performance, analyzing brain responses to later false alarms and correct rejections could not support this assumption.

In summary, we gathered first evidence for answering our second research question of what impact different memory consolidation strategies have on neural processing of mnemonic PEs and subsequent memory retrieval. Our findings from **Study 2** suggest that a rise in brain activity is associated with less solid memories stemming from higher cognitive demands. Nonetheless, more research is needed to understand the role of different consolidation strategies in episodic memory.

## 4.4 Future Prospects and Research

### 4.4.1 General Ideas

Similar brain structures were proposed to be involved during encoding and retrieval of episodic memories, like the hippocampus, PFC, and parietal cortex (Rugg et al., 2015). The present work focused on the neural mechanisms and behavioral outcomes of mnemonic PEs during episodic memory retrieval. To better understand the brain areas contributing to memory modification by encoding mismatching information, future studies should include fMRI recordings during initial encoding and later exposure to mnemonic PEs during retrieval. In our studies, we were able to show that original and modified episodes commonly increased activity in brain regions associated with episodic retrieval (**Studies 1** and **3**; also see Siestrup et al., 2022). Thus, it would be interesting to shed light on brain mechanisms contributing to the initial encoding of episodes and the encoding of mismatching or interfering information. For instance, memory modification was suggested to depend on neural coactivation of brain regions. Accordingly, strong coactivation was proposed to result in memory integration, while moderate coactivation rather leads to memory differentiation (Ritvo et al., 2019). This proposal is in line with findings from misinformation studies. When exposed to two sources of information, subjects are more likely to remember information that has undergone greater neural processing, regardless of whether it was originally or later falsely encoded (Baym & Gonsalves, 2010; Okado & Stark, 2005). Therefore, by defining neural patterns of original episodes, studies could localize brain regions involved in encoding false memories and/or updating existing memories.

Accordingly, the degree to which mnemonic PEs elucidate episodic memory modification may depend on initial memory strength (Exton-McGuinness et al., 2015; Fernández et al., 2016). Our studies demonstrated that our encoding procedure resulted in strong mnemonic representations as memory performance for originals remained largely intact. Therefore, it might be beneficial to vary initial memory strength by applying different numbers of presentation during encoding. In **Study 3**, we showed that repeated retrieval of a single alternative version was effective in brain and behavior while varying alternative versions did not impair later memory performance. During encoding, participants experienced original episodes five times, while alternatives were presented eight times when presented with a repetitive PE or two times with each varying version. Thus, we assume the memory strength of both original and modified episodes to play a crucial role when alternative information competes with existing memories.

### 4.4.2 Methodological Aspects

The episodic modification paradigm used in our studies was different from previous studies using rather simple stimuli and tasks. For example, in some studies, participants were supposed to remember pairs of words or objects (e.g., Chen et al., 2011; Duncan et al., 2009; Long et al., 2016), or static sceneries (e.g., Bein et al., 2020; Duncan et al., 2012; Ortiz-Tudela et al., 2017). Therefore, a major advantage of our paradigm lies in using dynamic, episodic videos to create a naturalistic situation of remembering an episode experienced in a controlled setting. Moreover, our encoding procedure strongly diverged from previous studies using encoding through a rather passive encoding of stimuli (Greve et al., 2017; Kim et al., 2014). In our studies, participants were highly attentive and personally involved during encoding. Irrespective of self-performance (**Studies 1** and **2**) or active observation (**Studies 1** and **3**), our findings repeatedly showed that participants actively encoded strong memories of presented episodes. However, encoding included multiple repetitions of observing and/or performing an action. In everyday life, episodic memories are not encountered repeatedly in the strict sense as they were in our experiments. Naturally, episodic memories are based on single encounters of a specific event (Cheng & Werning, 2016). Albeit our paradigm allowed strong encoding, it may not fully provide the natural encoding of episodes and needs to be improved.

Overall, behavioral evidence from our studies suggests that mnemonic PEs lead to the encoding of alternative episodes competing with existing memories (**Studies 1** and **2**). However, it remains unclear whether longer time lags between modification and memory testing may impair episodic memory retrieval of original episodes. In our studies, the post-fMRI memory test was conducted immediately (**Studies 1** and **2**) or one day (**Study** 3) after modifying episodes in the scanner. Memory retrieval was suggested to depend on gradual changes in context between one situation and another over time, including changes in environment, mood, and thoughts of a person (Roediger & Abel, 2022), potentially raising the likelihood of false memories in everyday life. In contrast, a greater amount of sleep over time may result in enhanced consolidation (Bosshardt, Schmidt, et al., 2005; Takashima et al., 2006), making memories more robust toward changes. Therefore, investigating the behavioral effects on episodic memory by applying longer time lags between experiencing modified episodes and post-fMRI testing might be fruitful to broaden our understanding of episodic memory modification over time.

Aside from that, it would be valuable for future research to link brain data to subsequent memory performance. Across our studies, we only provided limited evidence of brain-behavior interaction (**Study 2**) as we mainly focused on investigating neural differences during the experience of original and modified episodes (**Studies 1**, **2**, and **3**). For instance, we could not test memory on modified versions in **Study 3** as we only tested original object recall. To investigate the relationship between neural responses to mnemonic PEs and memory modification, episodic memory studies should incorporate testing both true and false memories. In recent years, a few studies have demonstrated a link between greater brain activation and later retrieval of false versus true memories (e.g., Baym & Gonsalves, 2010; Okado & Stark, 2005; St. Jacques, Olm, et al., 2013). However, other studies failed to establish a clear association between brain activation and false memory formation (Siestrup et al., 2022; Sinclair et al., 2021). Therefore, future research should consider optimizing episodic modification paradigms and using appropriate statistical methods to analyze how different brain regions encode later true and false memories. One possibility thereof could be using representational similarity analysis (Kriegeskorte et al., 2008) to identify similar neural patterns between original and modified episodes, and to link brain and behavioral data.

### 4.4.3 Self-Referential Factors

**Study 1** offered first insights into how self-referential factors may influence the encoding and retrieval of episodic memory. However, our results do not provide clear evidence for strong benefits of self-performance or 1pp, as derived from previous research on agentive states (cf. section 1.3.2) and visual perspective (cf. section 1.3.1).

Regarding the factor agency, additional work is needed to illuminate how agentive states influence neural activation and learning from PEs. Future studies investigating agentive states in episodic memory should focus on specific brain areas that are conceptually linked to the enactment effect. For instance, neuroimaging studies found increased activity in SMG during retrieval of self-performed actions (Krönke et al., 2013; Nyberg et al., 2001; Russ et al., 2003). Russ et al. (2003) suggested SMG to reflect the integration of motor plans and object knowledge into a coherent action representation. This integrative function is further supported by findings showing increased activity of SMG, as well as the premotor cortex, when planning to perform an action later in time (Eschen et al., 2007). As this region was mainly found in studies contrasting self-performed with verbal tasks (Krönke et al., 2013;

Nyberg et al., 2001; Russ et al., 2003), it remains unclear whether ROI analysis of SMG would lead to differential brain activation for previously self-performed versus only observed episodes. Neuroimaging studies investigating the enactment effect are typically conducted during retrieval as enacted trials during encoding would lead to body movement artifacts, i.e., high levels of noise in data. Therefore, future research could use navigation tasks in virtual reality (cf. section 4.3.1) and motor imagery (e.g., Naito et al., 2002) to potentially bypass this problem.

Remembering episodes from the past may occur from both 1pp and 3pp (e.g., Nigro & Neisser, 1983; Rice & Rubin, 2009). Therefore, it is difficult to draw any definitive conclusions from studies reporting a lack of differential brain responses resulting from 1pp versus 3pp (e.g., **Study 1**, Leynes et al., 2017). Nonetheless, they also raise several unresolved questions on how encoding or retrieval perspective may influence the mnemonic replay and subsequent memory performance of personally experienced episodes. One question is whether encoding perspective influences neural responses of later retrieval perspective. Although some researchers argued that 3pp memories might be formed during memory encoding (McCarroll, 2017; Nigro & Neisser, 1983), it remains an open issue whether perspective can be preserved and later retrieved. Therefore, it may be fruitful to conduct fMRI studies including scanning during encoding and retrieval of naturalistic episodes. Accordingly, future studies should clarify to what extent differential brain networks contribute to retrieving one or shifting to another perspective. To this end, episodes could be encoded and retrieved in one perspective (scheme: 1pp – 1pp / 3pp – 3pp) or later retrieved from another perspective (1pp – 3pp / 3pp – 1pp). Another question is whether the time lag between encoding and testing affects memory performance resulting from 1pp versus 3pp. While encoding perspective was reported to affect memory performance immediately after encoding in one study (Leynes et al., 2017), another study found differences only after a one-week delay (Bergouignan et al., 2014). Moreover, an important question is how autonoetic consciousness influences encoding and retrieval perspective in episodic memory. The subjective experience of self in time was suggested to characterize episodic memory (Gardiner, 2001; Tulving, 2005). Beneficial effects of a 1pp (versus 3pp) were suggested to depend on subjective vividness during retrieval (Marcotti & St. Jacques, 2018; Rice & Rubin, 2009). One question is how bodily self-awareness (Blanke, 2012; Blanke et al., 2015), i.e., the experience of body ownership and self-location, contributes to retrieval perspective and memory performance for personally experienced episodes. Initial findings suggest that virtual environments are a promising tool to address this self-referential feature in naturalistic episodes during both encoding and retrieval from 1pp (Gauthier et al., 2020; Shin et al., 2022) as well as 3pp (Iriye & St. Jacques, 2021).

# 5 Conclusion

This present thesis investigated the interplay between mnemonic PEs and episodic memory, illuminating their neural substrates and behavioral outcomes. A series of fMRI studies presented highly replicable evidence that mnemonic PEs trigger increased brain responses characterizing expectation violation and memory updating. Across studies, mnemonic PEs repeatedly elicited increased brain activity in vlPFC (IFG/IFS) and IPS/SPL, especially when exposed to varying PEs, highlighting their role in episodic mismatch detection and selective processes in episodic memory retrieval. Repeated encounters of (repetitive) PEs, impaired memory retrieval of original episodes and led to a strong tendency to misclassify modified episodes as originally encoded. Further, increased hippocampal and ACC activity over time predicted later false memories, indicating their role in PE-based memory updating. Moreover, we were the first to demonstrate the nuanced effects of agency, perspective, and consolidation practice on episodic memory using unique, multi-step episodes, underscoring the complexity of memory processes and the need for further research.

In summary, the presented findings contribute to our understanding of neural responses underlying and behavioral outcomes resulting from mnemonic PEs. Mnemonic PEs interact with original memories during retrieval of complex, naturalistic episodes. Repeated encounters of the same PE trigger episodic mismatch signals in the brain and can confuse subsequent memory retrieval, possibly stemming from alternative versions of the same memory trace. Against this background, the imperfection present in our episodic memory system is highly functional, allowing us to maintain predictive success in an ever-changing world. Nonetheless, future research needs to further investigate the conditions rendering learning from PEs.

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# Abbreviations

| | |
|---|---|
| 1pp | first-person perspective; field perspective |
| 3pp | third-person perspective; observer perspective |
| BA | Brodmann area |
| ACC | anterior cingulate cortex |
| BOLD | blood oxygenation level-dependent |
| fMRI | functional magnetic resonance imaging |
| HERA | Hemispheric Encoding Retrieval Asymmetry |
| IFG | inferior frontal gyrus |
| IFS | inferior frontal sulcus |
| IPS | inferior parietal sulcus |
| mPFC | medial prefrontal cortex |
| MTL | medial temporal lobe |
| MTT | Multiple Trace Theory |
| PE(s) | prediction error(s) |
| PFC | prefrontal cortex |
| pCC | posterior cingulate cortex |
| PPC | posterior parietal cortex |
| ROI | region of interest |
| SCT | Standard Consolidation Theory |
| SMG | supramarginal gyrus |
| SPL | superior parietal lobe |
| vlPFC | ventrolateral prefrontal cortex |

# Curriculum Vitae

## Personal Details

Name: Benjamin Tobias Jainta

Date of Birth: 03. Oktober 1992

Place of Birth: Gütersloh

## Academic Career

| | |
|---|---|
| Since 10/2019 | Research associate and doctoral student, Biological Psychology, University of Münster |
| 04/2017 – 09/2019 | Master of Science Psychology, University of Würzburg |
| 02/2016 – 07/2016 | Bachelor of Science Psychology, University of Warsaw |
| 10/2012 – 03/2017 | Bachelor of Science Psychology, University of Würzburg |
| 08/2009 – 06/2012 | Abitur, Städtisches Gymnasium, Gütersloh |

## Teaching Experience

| | |
|---|---|
| 2020 | Biological Psychology Seminar, M.Sc. Psychology, University of Münster |
| 2021 | Biological Psychology Seminar, M.Sc. Psychology, University of Münster |
| 2022 | Biological Psychology Seminar, M.Sc. Psychology, University of Münster |

## Awards

| | |
|---|---|
| 2016 | Scholarship from Gemeinschaft für studentischen Austausch in Mittel- und Osteuropa (GFPS) e.V. |
| 2014 | Scholarship from Friedrich-Ebert-Stiftung (FES) e.V. |

## Publications and Conference Presentations

**Jainta, B.**, Zahedi, A., & Schubotz, R.I. (in press). Same same, but different: Brain areas underlying the learning from repetitive episodic prediction errors. *Journal of Cognitive Neuroscience.*

Selvan, R. N., Cheng, M., Siestrup, S., Mecklenbrauck, F., **Jainta, B.**, … Schubotz, R. I. (2024). Updating predictions in a complex repertoire of actions and its neural representation. *NeuroImage*, 120687. https://doi.org/10.1016/j.neuroimage.2024.120687

Siestrup, S., **Jainta, B.**, Cheng, S., & Schubotz, R. I. (2023). Solidity Meets Surprise: Cerebral and Behavioral Effects of Learning from Episodic Prediction Errors. *Journal of Cognitive Neuroscience, 35*(2), 291-313. https://doi.org/10.1162/jocn_a_01948

**Jainta, B.**, Siestrup, S., El-Sourani, N., Trempler, I., Wurm, M.F., Werning, M., Cheng, S., Schubotz, R.I. (2022) Seeing what I did (not): Cerebral and behavioral effects of agency and perspective on episodic memory re-activation. *Poster at the 29th Annual Meeting of the Cognitive Neuroscience Society*. San Francisco, USA.

Siestrup, S., **Jainta, B.**, El-Sourani, N., Trempler, I., Wurm, M. F., Wolf, O. T., ... & Schubotz, R. I. (2022). What happened when? Cerebral processing of modified structure and content in episodic cueing. *Journal of Cognitive Neuroscience, 34*(7), 1287-1305. https://doi.org/10.1162/jocn_a_01862

**Jainta, B.**, Siestrup, S., El-Sourani, N., Trempler, I., Wurm, M. F., Werning, M., ... & Schubotz, R. I. (2022). Seeing what I did (not): Cerebral and behavioral effects of agency and perspective on episodic memory re-activation. *Frontiers in Behavioral Neuroscience, 15*, 353. https://doi.org/10.3389/fnbeh.2021.793115

**Jainta, B.**, Siestrup, S., El-Sourani, N., Trempler, I., Wurm, M.F., Werning, M., Cheng, S., Schubotz, R.I. (2022) When I (do not) see myself: The role of agency and perspective in episodic memory. *Talk at the 64th Tagung experimentell arbeitender Psychologen (TeaP)*. Köln, Germany. (Virtual conference; VC)

**Jainta, B.**, Siestrup, S., Schubotz, R.I. (2021). Investigating the effect of self-perspective and self-performance on episodic memory retrieval. *Talk at the Generative Episodic Memory: Interdisciplinary perspectives from neuroscience, psychology and philosophy 2021* (GEM) 2021. Bochum, Germany. (VC)

# Declarations

Declarations by the candidate documenting **open-science activities** and **on the consideration of ethical aspects** as part of the doctoral process and disclosure of **personal contribution** for manuscripts completed by two or more authors (cumulative dissertations)

Doctoral candidate: Benjamin Tobias Jainta

Title of dissertation: The Effects of Encoding, Retrieval, and Modification on Episodic Memory - Neural Substrates and Behavioral Consequences of Prediction Errors

## 1. Documentation of **open-science activities**

Manuscript 1

| | yes | no | If yes, please specify the source |
|---|---|---|---|
| | | | |
| Pre-registration | | X | |
| Publication of data | | X | |
| Publication of analysis scripts | | X | |
| Publication of materials | | X | |
| Open access publication | X | | https://doi.org/10.3389/fnbeh.2021.793115 |

Manuscript 2

| | yes | no | If yes, please specify the source |
|---|---|---|---|
| | | | |
| Pre-registration | | X | |
| Publication of data | | X | |
| Publication of analysis scripts | | X | |
| Publication of materials | | X | |
| Open access publication | | X | |

Manuscript 3

| | yes | no | If yes, please specify the source |
|---|---|---|---|
| | | | |
| Pre-registration | | X | |
| Publication of data | | X | |
| Publication of analysis scripts | | X | |
| Publication of materials | | X | |
| Open access publication | | X | |

## 2. Declaration on **the consideration of ethical aspects**

| **Study number** | **Source (manuscript / chapter of dissertation):** e.g. study 1 in paper 2, study 1 described in chapter 4 | **Was the study reviewed by an ethics commission?** | |
|---|---|---|---|
| | | **yes** | **no** |
| 1 | Manuscript 1 | X | |
| 2 | Manuscript 2 | X | |
| 3 | Manuscript 3 | X | |

## **3. Declaration** of one's **personal contribution** to the submitted academic manuscripts by two or more authors

### Manuscript 1

| | |
|---|---|
| Title | Seeing What I Did (Not): Cerebral and Behavioral Effects of Agency and Perspective on Episodic Memory Re-activation |
| Author(s) | Benjamin Jainta, Sophie Siestrup, Nadiya El-Sourani, Ima Trempler, Moritz F. Wurm, Markus Werning, Sen Cheng, & Ricarda I. Schubotz |

| | | | |
|---|---|---|---|
| Publication status: | not yet submitted | | (please mark with X) |
| | submitted | | |
| | in review | | |
| | in revision | | |
| | accepted | | |
| | published | X | |

| | |
|---|---|
| Journal | Frontiers in Behavioral Neuroscience |
| Year of publication | 2022 |

Description of your own contribution in the case of joint authorship:

- partly responsible for the study's conception and design
- partly responsible for data collection
- mainly processing, analyzing and interpreting data
- mainly responsible for writing and revising the manuscript
- marked as corresponding author

**Manuscript 2**

| | | | |
|---|---|---|---|
| Title | Solidity Meets Surprise: Cerebral and Behavioral Effects of Learning from Episodic Prediction Errors | | |
| Author(s) | Sophie Siestrup, Benjamin Jainta, Sen Cheng, & Ricarda I. Schubotz | | |
| Publication status: | not yet submitted | ☐ | (please mark with X) |
| | submitted | ☐ | |
| | in review | ☐ | |
| | in revision | ☐ | |
| | accepted | ☐ | |
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| Journal | Journal of Cognitive Neuroscience | | |
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| Description of your own contribution in the case of joint authorship:<br>- partly responsible for the study's conception and design<br>- partly responsible for data collection<br>- partly responsible for processing, analyzing and interpreting data<br>- partly responsible for responsible for writing and revising the manuscript | | | |

**Manuscript 3**

| | | | |
|---|---|---|---|
| Title | Same same, but different: Brain areas underlying the learning from repetitive episodic prediction errors | | |
| Author(s) | Benjamin Jainta, Anoushiravan Zahedi & Ricarda I. Schubotz | | |
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Description of your own contribution in the case of joint authorship:

- partly responsible for the study's conception and design
- mainly responsible collecting, processing, analyzing and interpreting data
- mainly responsible for writing and revising the manuscript
- marked as corresponding author

Münster, 28.06.2024

Place, Date

B.

Signature of the doctoral candidate