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Memory strength at reactivation, not memory age, governs prediction error-driven updating of naturalistic event memory

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Prediction error during memory reactivation is posited to be a key driver of memory updating. However, prediction error leads to varied memory outcomes, and it is unclear what specific factors influence memory malleability. Two factors have long been theorized to shape a memory's susceptibility to modification—the age and strength of the memory at reactivation—but their interaction with prediction error has not been directly tested in complex, naturalistic events. In a three-session paradigm using short videos with salient action–outcome narratives, we elicited prediction error by interrupting expected outcome endings during reactivation. Following reactivation, participants viewed semantically similar videos introducing new information that could be incorporated into an updated memory. Memory age was manipulated by varying the delay between encoding and reactivation (1 h, 24 h or 2 weeks) and memory strength was measured with participants' ratings of recollection quality after each video reactivation. We found that prediction error at reactivation selectively increased the intrusion of newly experienced information for weak, but not strong, memories at reactivation. By contrast, the age of a memory at reactivation neither interacted with prediction error nor influenced memory outcomes. These findings identify memory strength, not age, as the critical boundary condition for prediction error-driven memory updating in human episodic memory.

This article is part of the theme issue 'The role of hippocampal predictions in cognition: bridging perception and memory'.

1. Introduction

Unlike images captured by a camera, the records stored in our episodic memory can change as a function of time and experience. Prediction error—or the mismatch between what we expect based on a reactivated memory and what actually occurs—has been posited as a key signal for memory updating [1–5]. By signalling a gap between expectation and reality, prediction error may prompt a reactivated memory to update and incorporate novel information [2,5]. However, not all prediction errors lead to memory updating, and conversely, memory updating can occur even in the absence of overt prediction errors. From an adaptive perspective, this makes intuitive sense: not every violated expectation should lead to a memory change. In many cases, it would be maladaptive to alter a well-formed, accurate memory simply because an anticipated outcome did not occur. A central question, then, is what factors shape whether prediction error drives memory updating, which we define as any changes in the reported content of a memory that reflect new experiences following its reactivation. Here, we investigate the

independent contributions of two such factors that are often confounded in previous work: the age and strength of a memory at reactivation.

The age of the memory has been shown to be a prominent factor determining a memory's susceptibility to updating [6–12]. Grounded in systems consolidation theories and time-dependent stabilization, older memories are thought to become increasingly resistant to modification as they transition from hippocampal to neocortical dependence [13–17]. In support of this view, rodent studies have shown that recent memories (e.g. 24 h after encoding) do not require a prediction error to update, whereas older memories (e.g. 48 h) update only when a prediction error is present [11,18,19]. By contrast, the few human studies that have manipulated memory age at reactivation have reported mixed findings regarding whether recent or older memories are more susceptible to change [20–25]. These discordant results may reflect experimental design differences, including variation in delay intervals, stimulus types and procedures used to reactivate memories and introduce interfering information [2,5,21–24,26–30]. Importantly, none of the studies directly examined how memory age interacts with prediction error. As a result, the role of memory age in shaping prediction error-driven updating in humans, particularly for detailed episodic memories, remains unresolved.

A critical factor that may clarify these findings is memory strength at the time of reactivation. Memory age is often confounded with memory strength; specifically, as older memories tend to be weaker than more recent ones, it has been difficult to determine whether susceptibility to updating reflects elapsed time or the strength of the memory when it is reactivated. Across species, weak memories are more readily updated than strong ones [12,25,31–33], with the prominent nonmonotonic plasticity hypothesis proposing that moderately reactivated memories are most susceptible to change [34,35]. What is less clear is how memory strength interacts with prediction errors. In rodents, strongly but not weakly encoded memories are resistant to updating [10,11,36,37], and such strong memories require prediction error to be destabilized and updated [11,32,38–40]. However, a recent theory of human memory—the event memory retrieval and comparison theory (EMRC)—argues the opposite: that is, it suggests that strong, but not weak, memories are impervious to (or even strengthened by) prediction error [28,41]. Under this view, having a strong memory of the initial experience facilitates change detection upon prediction error, leading to the formation of recursive memory representations that integrate the initial event, the experience of the prediction error and the new outcome. Because these recursive memories distinctly represent both initial and new experiences, strong memories at reactivation are protected and even strengthened by prediction errors. However, when the initial memory is weak, prediction error may instead drive interference, updating the memory with competing new content. Consistent with this framework, recent studies using naturalistic narrative video stimuli have shown that stronger initial memory—indexed by predictive eye gaze [42] or neural reinstatement at reactivation [43]—predicts better subsequent memory for changed event features. These paradigms introduce prediction errors by changing a specific point in the narrative, while the other parts remain identical, and subsequently test the retrieval of the changed content. Focusing on memory for the specific features that change leaves open the question of how prediction error influences memory for the broader event representation. Taken together, despite growing interest in how memory strength shapes its malleability [44–47], the field has yet to resolve a central question: whether prediction error modifies existing memories or instead protects them from change.

Our study addresses these open questions regarding how memory age and strength interact with prediction error by adapting a naturalistic memory-updating paradigm [48,49] to manipulate the age of a memory and measure the strength of a memory at reactivation. Prior work using this paradigm has shown that prediction error both drives memory updating and determines the relationship between hippocampal activation and memory outcomes. Specifically, greater hippocampal activity following prediction error led to updating, whereas greater hippocampal activity in the absence of prediction error led to strengthening [48]. Building on this work, our paradigm consisted of three sessions (figure 1) and leveraged naturalistic stimuli to increase the generalizability of our findings, given that the consolidation of event memories connected to schematic knowledge can differ from that of the arbitrary associations used in traditional lab-based stimuli [50]. First, participants encoded short video clips featuring salient action–outcome sequences designed to generate a strong sense of anticipation. Second, after a delay of 1 h, 24 h or 2 weeks (assigned between subjects), these videos were reactivated, after which participants rated their memory strength. Critically, reactivation occurred either with prediction error (the anticipated ending was interrupted, creating a jarring sense of surprise) or without prediction error (the full video was shown). Shortly after reactivation, participants viewed a set of semantically related interference videos. In the third and final session, participants' memories for the encoded videos from Session 1 were assessed through structured memory interviews, which were scored for correct details and errors (with errors coded as either intrusion details from videos in the experiment or false details from unknown sources).

Our approach overcomes the common confounding of age and strength in memory-updating research, leverages subjective memory assessments that are unique to humans and extends prior work by directly testing the relationship between prediction error and memory age. In doing so, this work bridges findings from rodent and human studies, clarifying how memory age and strength shape susceptibility to change and determine when prediction error drives updating. Our primary finding was that prediction error selectively induced intrusions in weak but not strong memories at reactivation. By contrast, the effect of prediction error was not influenced by the age of the memory at reactivation. Together, these patterns of results suggest that in the context of naturalistic event stimuli, the outcomes of prediction error-driven updating are shaped by memory strength at reactivation rather than by time-dependent consolidation, specifically supporting frameworks in which strong memories are protected from, rather than modified by, prediction error.

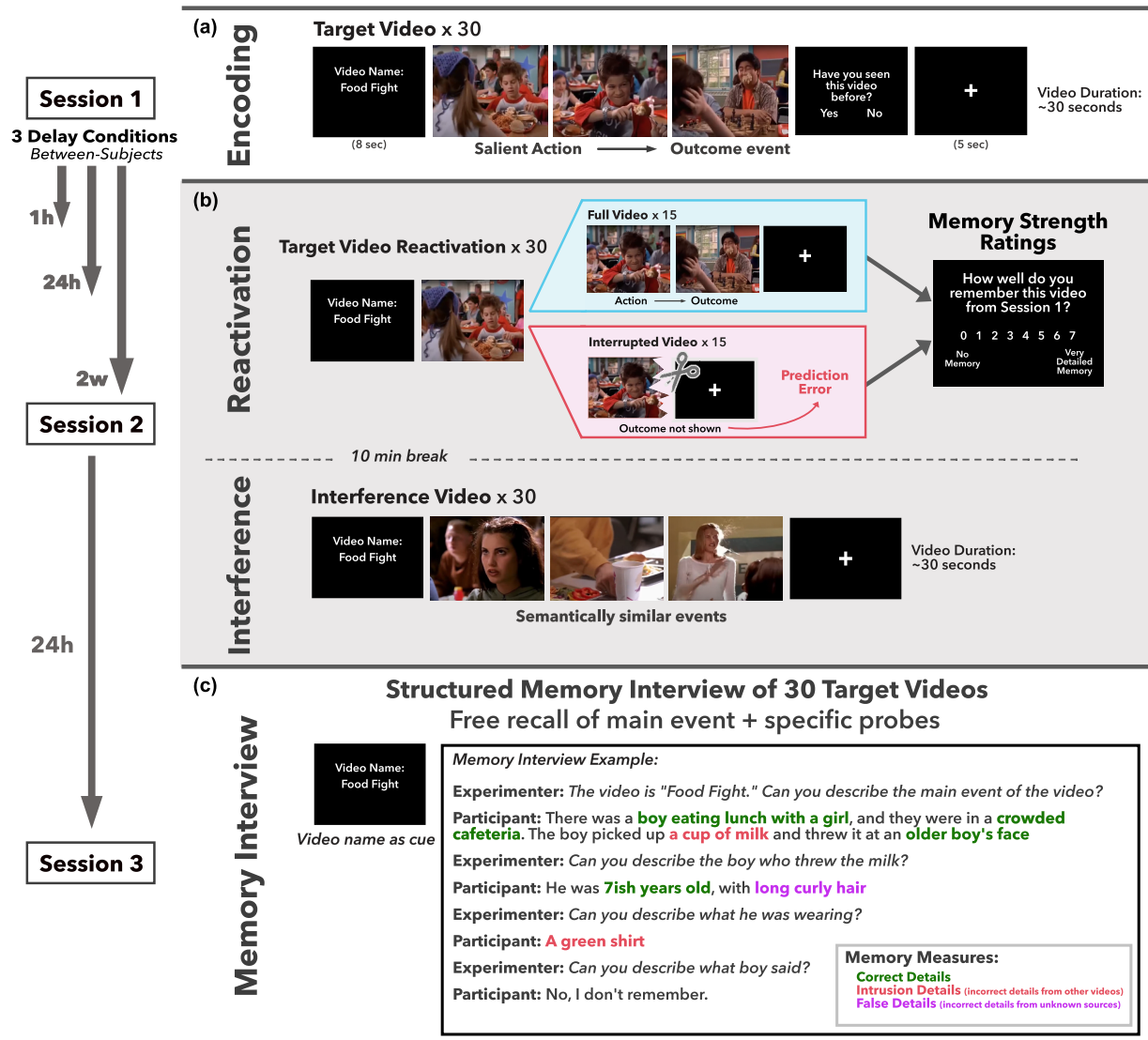


Figure 1. Overview of the three-session design. (a) In Session 1, participants encoded 30 target videos, which featured a salient action followed by its outcome. (b) In Session 2 (following a 1 h, 24 h or 2 week delay), all videos were reactivated—either with or without prediction error (15 videos per condition)—and new interfering videos were introduced. To generate prediction error, Interrupted videos ended after the action but before the outcome of the event, inducing a jarring sense of surprise. After watching each target video, participants rated their memory strength for the original video from Session 1. Following a 10 min break, participants viewed interference videos that featured semantically similar events but varied in specific details, such as characters and setting. (c) In Session 3 (24 h delay), participants completed a structured memory interview for all 30 target videos, which included free recall of the entire video and specific follow-up probes. Recall responses were scored for correct details, intrusion details (could be traced to another stimulus video) and false details (could not be directly traced to any stimulus videos). Here, we present examples of interview questions and responses, along with the scoring of correct details, intrusion details and false details.

2. Methods

(a) Participants

We recruited 156 paid participants between the ages of 18 and 35 years old from the University of Toronto community. The final sample size consisted of 114 participants, after excluding those who failed to complete all study sessions ($n = 33$) and those who experienced technical difficulties during study sessions ($n = 9$). Participants were young adults (mean age = 21.2 years, s.d. age = 3.23 years, age range = 18–30 years; 99 self-identified female, 14 self-identified male, 1 declined to answer) and ethnically heterogeneous: South Asian 29, East Asian 30, White 23, Southeast Asian 7, Black 8, Middle Eastern 5, Arab 2, Latin American 1, declined to answer 9. On average, participants had 15 years of education (s.d. = 2.05 years, range = 11–23 years), calculated as the total number of years of formal schooling from Grade 1 onward, including both secondary and post-secondary education. All participants met the inclusion criteria: normal corrected to normal vision and hearing, no reported history of psychological or neurological disorders or brain damage and fluency in English. All participants provided written informed consent prior to the study and received monetary compensation for their participation. The study was approved by the Research Ethics Board at the University of Toronto.

For our sample size determination, the novelty of our manipulations limited the applicability of prior findings for a power analysis. Therefore, we adopted a sequential design with two pre-specified interim analyses and stopping criteria to permit flexible recruitment without compromising rigour [51]. We set the minimum sample size at 114 participants (38 per delay

condition) to detect the effect of prediction error with 80% power at 24 h delay (Cohen's $d = 0.6$) [49]. We set the maximum sample size at 180 participants based on resource and feasibility constraints and an interim stopping point at 147 participants. We planned interim analyses at each of these stopping points to evaluate evidence for the memory age by prediction error interaction, a central effect examined in the study. Evidence was assessed using Bayes factors derived from Bayesian model comparisons with and without the interaction term, allowing us to determine whether there was substantial evidence for the interaction or for the null model excluding it. Data collection continued until this criterion was met. Substantial evidence was reached at the minimum planned sample size, satisfying our pre-specified stopping criteria, and recruitment was therefore concluded.

(b) Design

We implemented a three-session study to investigate memory updating using naturalistic stimuli consisting of short live-action video clips (figure 1). We expanded the study procedures from a prior prediction error paradigm [49] by introducing two additional factors: the age of the memory and the strength of the memory at its reactivation. Memory age was manipulated between-subjects by assigning each participant to one of three delays between memory encoding and reactivation (1 h, 24 h and 2 w). Memory strength was measured within-participants via subjective ratings at memory reactivation for each individual memory. Prediction error, which we kept unchanged from the prior paradigm, also varied within-subject, with videos reactivated with or without prediction error. Prediction error was operationalized by interrupting the video at a salient action–outcome sequence, thereby violating participants' expectations about the video's outcome scene, analogous to disrupting a learnt conditioned stimulus–unconditioned stimulus (CS–US) contingency in classical conditioning paradigms [5].

In Session 1, participants encoded a set of video clips and then experienced one of three delays (1 h, 24 h or 2 week). In Session 2, each participant reactivated previously encoded videos either with (Interrupted) or without (Full-length) a prediction error (15 videos per condition), and, after each of the 30 videos, they rated how well they remembered it from Session 1. After a short break, participants were then presented with semantically related interference videos designed to elicit intrusions into memories susceptible to modification. All participants then returned 24 h later for Session 3, during which they completed a structured verbal memory interview about the Session 1 videos. Memory interview transcripts were coded and scored for correct details and for incorrect details characteristic of memory updating.

The delays were selected to sample memories across early and later post-encoding intervals examined in memory consolidation research, with the 1 h delay primarily reflecting early cellular consolidation, the 24 h delay capturing the transition toward systems-level consolidation and the 2 week delay reflecting more extended systems consolidation [6,52–56]. The 24 h delay also allowed for close comparison with the prior paradigm that we adapted [49].

(c) Stimuli

The stimulus set consisted of 60 videos organized into 30 semantically related pairs, each comprising a target video and a corresponding interference video. The videos in each target–interference pair featured distinct characters and settings, as well as variations in plot progression, but they shared a common overarching narrative theme (e.g. Food Fight pair: both videos depicted a character picking up and throwing food at another character) and were labelled with the same title that described the central situation or activity (e.g. 'Food Fight'). All videos were approximately 30 s long (duration $M = 32.5$ s, $s.d. = 5.5$ s) and were sourced from online English-language films and television shows. The videos included salient action–outcome sequences (e.g. a character throws food, resulting in another character being hit with food).

To elicit prediction error, we violated expectations for the action–outcome sequence by abruptly ending target videos at their narrative climax points, thereby omitting the salient outcomes (e.g. video ended with the character mid-throw with food in hand). Prior studies have shown that this method of eliciting prediction error through interrupting videos is effective in inducing subsequent memory updating [48,49]. For each of the 60 videos, we created a prediction error version by excluding the ending segment of the video that contained the outcome sequence (duration $M = 23.8$ s, $s.d. = 5.4$). Across participants, we counterbalanced which member of each video pair served as the target versus the interference video and whether a video was shown in its Full or Interrupted version.

(d) Procedure

The study consisted of three sessions: (i) initial encoding of target videos, (ii) reactivation of target videos and viewing of interference videos, and (iii) verbal recall of target videos. All sessions were conducted on desktop computers using PsychoPy (v. 2023.1.3) [57]. To maintain contextual consistency, participants completed all three study sessions in the same testing room and with the same experimenter. During Session 1 and Session 2, participants watched the videos alone in the testing room, whereas in Session 3, participants worked with the experimenter to complete the structured memory interview. During instructions for Session 1, participants were explicitly directed to pay close attention to both the video titles and content because their memory for these videos would be tested later using the video titles as retrieval cues. However, they were not informed about the specific test format. For all sessions, the experimenter reviewed the instructions and walked participants through a practice trial.

(e) Session 1: encoding

During encoding, participants viewed 30 target videos in a randomized order. Before each video, the title was centrally presented on the screen for 8 s and the title remained displayed below the video during playback. After each video, participants were instructed to indicate whether they had seen the video prior to the experiment by pressing a yes/no button (videos indicated as previously seen were excluded from analysis; 3% of trials were excluded). This was followed by presentation of a 5 s fixation cross before the sequence repeated for the next video.

(f) Session 2: memory reactivation and interference

Participants returned for Session 2 after one of three delays (1 h, 24 h or 2 week), which were randomly assigned during the recruitment process. Session 2 consisted of two parts: (i) memory reactivation of target videos and (ii) a short break, followed by presentation of interference videos. During reactivation, participants were informed that the target videos from Session 1 would be repeated and were asked to pay attention to the video titles and content. They were neither told about the prediction error manipulation, nor were there indicators of whether the video would be played in its Full (without prediction error) or Interrupted (with prediction error) version. A series of questions asked at the end of Session 3 indicated that all participants were aware of, but unable to anticipate, the occurrence of an interrupted ending.

Each participant watched 15 Full and 15 Interrupted target videos, presented in one of six pseudo-randomized sequences that were counterbalanced across participants. The first video in these sequences was always in its Full version, and no more than two Interrupted videos were shown consecutively. The presentation format in Session 2 was similar to Session 1, except after each video (Full or Interrupted), participants viewed a fixation cross for 5 s and were then prompted to rate how well they remembered the target video from Session 1 on a 0–7 point scale. A rating of 0 meant that the participant had no recollection of the video and felt that they were watching it as if for the first time, whereas a rating of 7 meant that they remembered the video in great detail. We used these ratings as our measure of participants' memory strength for each video. Trials with ratings of 0 and 1 were excluded (2.6% of trials) because these reflected little to no memory for the video from Session 1 and probably did not involve meaningful reactivation, but rather were more akin to a new encoding experience. Separately, memory strength ratings did not reliably differ between Full and Interrupted videos (electronic supplementary material, figure S1), indicating that viewing the ending scenes in the Full condition did not inflate ratings.

Once participants finished viewing all 30 target videos, they were asked to take a 10 min break, during which they completed the Pittsburgh sleep quality index [58] and left the testing room for water and washroom breaks. After the break, participants were presented with 30 interference videos and were asked to pay close attention to the video content and title, as they had during the initial encoding. Participants were informed that they would see the same video titles, but the corresponding videos would be entirely novel. After watching the interference videos, all participants were asked to return the next day for the final memory interview.

(g) Session 3: structured memory interview

In the final session, participants completed a structured memory interview on the 30 target videos that they had viewed in their full length versions during Session 1. Participants were instructed to recall the target videos in their entirety, regardless of whether the video had been reactivated in its Full or Interrupted form. Interference videos were not tested because the present study focused on memory updating for the originally encoded videos, and practical time constraints limited the testing of both sets of videos. This approach is consistent with the original prediction error paradigm that we adapted for the present work [49].

The recall order of the videos was randomized by the testing software. At the start of the interview, the experimenter gave participants detailed instructions on the interview process and walked them through the procedures and sample questions using a practice video. The audio from the memory interviews was recorded. For each video, participants were cued by the video title using the same screen as was shown in Sessions 1 and 2. They were then prompted to freely recall the video narrative. After the free recall, the experimenter followed up with a series of pre-determined questions to further probe details about the story, background and character details (e.g. *'Can you describe the setting?'*, *'Can you describe the physical appearance of the main character?'*). The experimenter adapted the pre-determined questions based on participants' responses and avoided introducing any video content that they had not already reported through the questions. For example, if a participant did not mention dogs in their recall, instead of asking the listed question *'What did the dogs look like?'*, the experimenter would use a more general prompt such as *'Can you describe anything else from the scene?'*. Conversely, if a participant spontaneously mentioned details that were not present in the video (e.g. describing a character who did not appear), the experimenter would still follow up with relevant questions (e.g. *'Can you describe what this character was wearing?'*) to further probe those memory details. Participants were explicitly instructed not to guess or confabulate any details, and instead to give void responses (*'I don't remember'*).

Following the verbal recall of each video, participants rated their overall memory on a 7-point scale in terms of its vividness, ease of recall and distinctiveness. At the end of the memory interview, the experimenter asked the participants several general questions about their experience of viewing the Interrupted videos during Session 2. Lastly, participants were debriefed.

On average, the memory interview lasted two and a half hours, with each video recall taking about 5 min to complete. No time limit was imposed for recalling each video. Given the long duration, participants were provided with water and light

snacks and allowed up to three 5 min breaks. Some participants ($n = 27$) took longer to complete the memory interview and, owing to time constraints, did not finish recalling all 30 videos. However, videos were rarely missed, with an average of 29 videos recalled per participant ($s.d. = 3$, range = 18–30).

(h) Memory interview scoring: detail types and procedure

We designed our memory scoring protocol based on previous adaptations of the autobiographical interview scoring method for narrative video memories [49,59–61]. Audio recordings of the structured memory interviews were first transcribed and then manually scored according to the presence of correct and incorrect details. Forgotten details were not scored (e.g. ‘I don’t remember what the character was wearing’).

Correct details referred to accurate recollections of elements that were present in the original target videos. Central event details as well as descriptive perceptual details were each counted as individual details (e.g. the statement ‘the boy threw a square slice of mushroom pizza’ would count as three details: one for the main action, ‘the boy threw pizza’, one for each descriptor, ‘square slice’ and ‘mushroom’). Correct details were scored independently from incorrect details, with no limit placed on the number of details participants could recall per video. Lower rates of correct details in a given condition were taken as an operational measure of memory weakening.

Incorrect details were subdivided into two categories: *intrusion details* and *false details*, which were summed to create a composite *total errors* measure. Intrusion details were incorrect memories that could be traced to a specific video (either the interference video or another video in the stimulus set) based on the details themselves and surrounding contextual information. Intrusion details were treated as our most direct operationalization of memory updating because they reflected integration of post-reactivation content. Given the narrow definition of intrusion details as source-identifiable incorrect details, we separately scored all other incorrect details that were random or ambiguous in video origin as false details.

In the stimulus set, there were overlapping event details between videos. Some were intentional—target–interference video pairs were chosen to be semantically similar (e.g. both videos show a food fight scene)—and others were unavoidable in a broad set of videos (e.g. common character attributes, background scenery). To maintain a conservative scoring approach, we treated these ambiguous instances with particular caution when determining whether they constituted intrusion details. Any reported detail that accurately reflected the contents of the target video was scored as correct, regardless of whether those details overlapped with another video. For example, if the target video depicted a boy sitting at a table and the corresponding interference video depicted an older woman sitting at a table, the recall of ‘a person sitting at a table’ would be scored as correct. Relatedly, incorrect details that were broadly shared across videos (e.g. multiple videos have characters with brown hair) were conservatively classified as false details when their source could not be determined. For example, in the recall ‘an older woman with brown hair was sitting at the table’, both ‘older woman’ and ‘brown hair’ inaccurately describe the target video. Because ‘older woman’ could be traced to the paired interference video, it was scored as an intrusion detail, whereas the more ambiguous feature ‘brown hair’, which could have originated from multiple videos, was scored as a false detail.

False details were taken to reflect either memory updating in the form of unrecognized intrusion details or memory weakening in the form of random errors. To account for the possibility that some false details could be intrusion details, a total errors measure (the sum of intrusion details and false details) was calculated to provide a more comprehensive index with greater sensitivity and statistical power for detecting overall modifications to the original memory. Thus, the total errors measure captures both memory updating in the form of inserted content, as well as memory weakening in the form of degraded content. This approach follows precedent in prior work indexing memory change using intrusion details alone [49], as well as total errors [48].

Videos were excluded from scoring when recall did not reflect memory for the target event. This included instances when the participant reported no recollection of any details, as well as instances in which participants recalled only the interference video without any details from the target video, or when they described a narrative that did not correspond to any video presented in the experiment (0.2% of trials). Finally, in order to minimize the influence of pre-existing knowledge on recall, videos were excluded when participants reported prior familiarity with the characters or the film or television show depicted, despite not having seen the specific clip (0.8% of trials).

Finally, we adapted our scoring procedures to account for the fact that the endings of videos in the Full reactivation condition were watched twice (during encoding and reactivation), whereas videos in the Interrupted condition were watched only once (during encoding). Thus, to ensure that the amount of exposure was equivalent across conditions, we restricted all analyses to details from portions of each target video that occurred before the interruption point, such that the assessed content had been viewed twice, regardless of reactivation condition. This pre-interruption segment comprised, on average, 89% of all recalled details for a given video (see electronic supplementary material, table S1, for analyses that include video endings). Detailed procedures and logistics for interview transcript scoring are provided in the electronic supplementary material.

3. Results

We analysed memory interview performance according to three dependent variables: intrusion details, total errors and correct details. We consider intrusion details to be the cleanest index of memory updating because these details reflect a change to the original memory based on quantifiable information that was introduced soon after the original memory was reactivated. However, intrusion details accounted for only 29% of total errors. As noted in §2, some false details represent unrecognized intrusions, given the inherent ambiguity in some of the sources of the recalled content. For this reason, we also examined total

errors as a more comprehensive measure of memory change, consistent with previous work [48]. Analyses on the false detail measure are additionally reported in the electronic supplementary material (electronic supplementary material, figure S3).

We used mixed-effects regression models in R (v. 4.2.2; RStudio v. 2022.12.0+353; R Core Team, 2022) to ask how memory updating was influenced by reactivation type (Full versus Interrupted video), memory age (1 h, 24 h or 2 w) and memory strength at reactivation. Reactivation type and memory age were modelled as categorical variables, and memory strength was modelled as a continuous variable. We ran separate models for each dependent variable: intrusion details (to assess memory updating), total errors (to more inclusively assess updating and weakening) and correct details (to assess memory weakening). These outcomes consisted of count data that were sparse, skewed and over-dispersed, and so we used negative binomial variants of mixed-effects models (R package: *glmmTMB* v. 1.1.10; [62]) to meet distributional assumptions. Each of the three models included two-way interactions (memory age $\times$ reactivation type and memory age $\times$ memory strength) along with random intercepts and random slopes to account for variability across participants and videos (see *electronic supplementary material, table S2 for model specifications*). Main effects and specific contrasts were examined using estimated marginal means derived from the fitted models (R package: *emmeans* v. 1.8.9; [63]). Below, we organize model results to focus, in turn, on the roles of reactivation type, delay and strength.

(a) Prediction error did not affect memory intrusions but increased total errors

We first sought to replicate prior findings that introducing a prediction error during memory reactivation increases the likelihood of memory updating, which we define as modifications to existing memories that reflect experiences subsequent to reactivation [48,49]. Using our most direct measure of updating—intrusion details—we found that participants did not recall significantly more intrusion details for Interrupted videos (i.e. memories reactivated with prediction error) compared with Full videos (i.e. memories reactivated without prediction error; main effect of reactivation type: $\beta = -0.07$, s.e. = 0.06, $z = -1.12$, 95% confidence interval (CI) $[-0.18, 0.05]$, $p = 0.26$; figure 2a). Although intrusion details were numerically higher for Interrupted videos, follow-up Bayesian model comparison provided strong evidence for the null, with the reduced model excluding the prediction error term being preferred over the full model (Bayes Factor, $BF_{01} = 3.3 \times 10^7$). Although this null was unexpected given prior work [49], it may reflect our more conservative scoring protocol, in which some intrusions of post-reactivation content may be coded as false details.

To assess this possibility, we next examined the broader measure of total errors, which captures both inserted and degraded content. Here, participants made significantly more total errors for Interrupted videos compared with Full videos (main effect of reactivation type: $\beta = -0.07$, s.e. = 0.03, $z = -2.08$, 95% CI $[-0.14, -0.004]$, $p = 0.038$; figure 2b), consistent with prior work [48]. Taken together, these findings provide mixed evidence that interruption-driven prediction errors promoted memory updating: the effect was not detectable in narrowly defined intrusions but emerged when using a less conservative measure that probably captures intrusions as well as general memory weakening.

(b) Prediction error decreased correct details

To further assess memory weakening, we turned to correct details. Participants recalled fewer correct details for Interrupted videos compared with Full videos (main effect of reactivation type: $\beta = 0.02$, s.e. = 0.01, $z = 2.49$, 95% CI $[0.004, 0.04]$, $p = 0.013$; figure 2c). Furthermore, videos recalled with fewer correct details were associated with more total errors ($\beta = -0.01$, s.e. = 0.003, $z = -2.16$, 95% CI $[-0.011, -0.001]$, $p = 0.031$).

Taken together, the analyses of correct and incorrect details suggest that prediction error at reactivation shapes subsequent memory by reducing the recall of correct details and increasing the number of total errors. However, the absence of an effect on intrusion details leaves its role in memory updating somewhat ambiguous. These complex findings could reflect important boundary conditions on prediction error-driven updating introduced by our experimental manipulations. Thus, we next examine the boundary conditions of memory age and strength at reactivation.

(c) The age of the memory had no effect on memory measures

Memory age did not act as a boundary condition on memory change (no main effect of memory age or age by reactivation type interaction across all three memory measures (intrusion details, total errors and correct details); figure 2d–f; see electronic supplementary material, table S3b). Furthermore, Bayesian model comparison provided strong evidence for the null, with the reduced model excluding memory age terms being strongly preferred over the full model across all memory measures (intrusion details: $BF_{01} = 3.7 \times 10^6$; total errors: $BF_{01} = 1.1 \times 10^9$; correct details: $BF_{01} = 5.0 \times 10^{11}$). There was also strong evidence against any memory age by reactivation type interaction (intrusion details: $BF_{01} = 2.2 \times 10^3$; total errors: $BF_{01} = 5.3 \times 10^3$; correct details: $BF_{01} = 9.8 \times 10^4$). Thus, while older memories were associated with lower memory strength ratings at reactivation (main effect of memory age: $\chi^2(2) = 30.59$, $p < 0.001$; see electronic supplementary material, figure S2), memory age did not directly affect final memory outcomes or the influence of prediction error—in contrast to prior findings in rodents [9–11].

The convergence of evidence across all three memory measures indicated that memory age did not influence a memory's susceptibility to change, with memories reactivated after 1 h, 24 h or 2 w all similarly susceptible to updating and comparable in terms of retention. Moreover, memory age did not influence the effect of prediction error on subsequent memory change.

Prediction Error has Differential Effects on Different Memory Measures

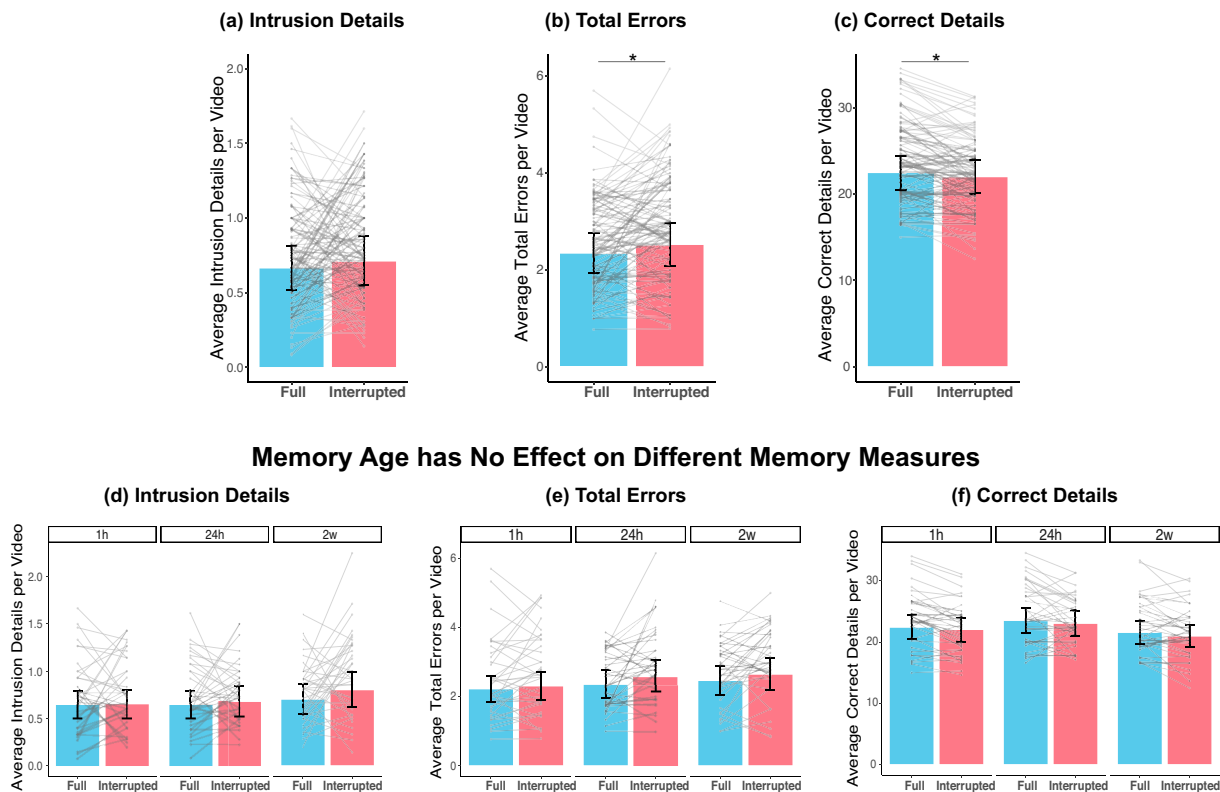


Figure 2. Top row: effects of prediction error (Full versus Interrupted video reactivation) collapsed across delay. Prediction error (Interrupted videos) did not increase (a) intrusion errors from the interference videos, but it did increase (b) total errors and reduce the number of (c) correct details recalled. Bottom row: effects of memory age (1 h, 24 h or 2 week delay between encoding and reactivation) on the same memory measures. Memory age did not affect (d) intrusion details, (e) total errors, or (f) correct details, and there were no interactions between delay and prediction error. Bars represent estimated marginal means from a negative binomial mixed-effects model. Participant averages are overlaid on top to display the distribution. * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$.

(d) Memory strength at reactivation influenced memory updating and recall

We next examined another important factor influencing memory updating—the perceived strength of the memory at the time of reactivation. We model memory strength as a linear predictor, given that quadratic models did not improve fit (see electronic supplementary material, table S4, for model comparisons).

Memory strength at reactivation significantly predicted later recall performance across all three measures (figure 3). Videos that were more strongly remembered at reactivation were later recalled with fewer intrusions (main effect of memory strength: $\beta = -0.06$, s.e. = 0.03, $z = -2.35$, 95% CI $[-0.11, -0.01]$, $p = 0.02$; see electronic supplementary material, table S3a), fewer total errors (main effect of memory strength: $\beta = -0.03$, s.e. = 0.01, $z = -2.14$, 95% CI $[-0.06, -0.002]$, $p = 0.033$) and more correct details (main effect of memory strength: $\beta = 0.02$, s.e. = 0.01, $z = 8.92$, 95% CI $[0.03, 0.05]$, $p < 0.0001$). As would be expected intuitively and from past work, these findings suggest that strong memory at reactivation was protective against memory modification—as evidenced by fewer incorrect details and more correct details.

The central question was whether and how memory strength at reactivation influenced the effect of prediction error on memory updating. For intrusion details, we found significant interactions between memory strength and reactivation type (interaction: $\beta = -0.10$, s.e. = 0.05, $z = -2.11$, 95% CI $[-0.20, -0.01]$, $p < 0.035$), such that Interrupted videos elicited more intrusions only when memory strength was low—that is, when participants perceived the memory for the original video as weak during reactivation (simple slope at low strength: $\beta = 0.18$, s.e. = 0.08, $z = 2.25$, 95% CI $[0.02, 0.33]$, $p = 0.024$). By contrast, when memory strength was high, the reactivation condition did not reliably influence later intrusion rates (simple slope at high strength: $\beta = -0.041$, s.e. = 0.08, $z = -0.52$, 95% CI $[-0.20, 0.12]$, $p = 0.60$). These findings point to the important interaction between prediction error and memory strength, specifically in updating weak memories selectively at reactivation. Notably, this interaction between strength and prediction error was selective to intrusion details; the relationship between prediction error and total errors and correct details did not significantly depend on memory strength (strength by reactivation type interaction for total errors: $\beta = 0.02$, s.e. = 0.03, $z = -0.61$, 95% CI $[-0.04, 0.07]$, $p = 0.54$; correct details: $\beta = -0.01$, s.e. = 0.01, $z = 1.36$, 95% CI $[-0.03, 0.01]$, $p = 0.17$).

Together, these findings suggest that memory strength acts as a boundary condition for the influence of prediction error on memory updating. Prediction errors appear capable of degrading memory representations—reducing accuracy and increasing overall errors—irrespective of how strongly a memory is reactivated. However, only when the strength of the memory is sufficiently low do prediction errors at reactivation promote intrusion of new details. In other words, prediction error may weaken all memories to some degree, but only weakly reactivated memories become sufficiently malleable to be updated with newly introduced content.

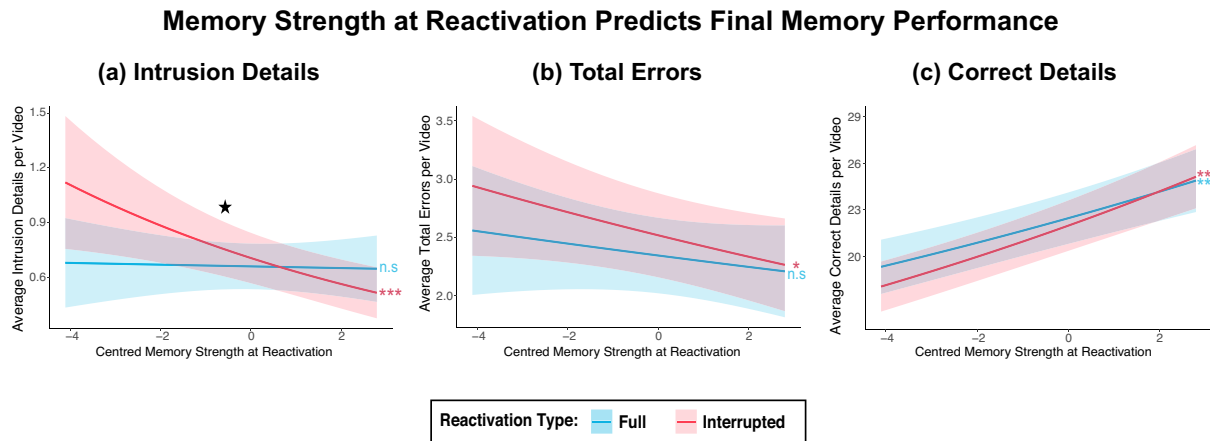


Figure 3. Memory strength at reactivation predicted memory outcomes. (a) Intrusion details: memory strength interacted with reactivation type (star indicates significant interaction). Higher memory strength predicted fewer intrusions only when reactivation was Interrupted (prediction error), with no relationship for Full reactivation. (b) Total errors: across both reactivation conditions, higher memory strength predicted fewer total errors; there was no interaction with prediction error. (c) Correct details: higher memory strength predicted more correct details for both reactivation conditions; no interaction was observed. Shaded bands represent 95% confidence intervals; memory strength values are person-mean centred. * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$.

4. Discussion

In this study, we investigated how two intrinsic memory features—memory strength and memory age at reactivation—interact with prediction error to produce different memory outcomes. Using a naturalistic movie-watching paradigm in which prediction error was elicited by interrupting highly expected endings of familiar narrative videos, we found that prediction error, in this context, has the capacity to weaken all memory to some extent, producing more total memory errors and fewer correct details, regardless of memory strength. By contrast, prediction error led to more memory updating, as captured by intrusion details from related videos, only in weak memories. Memory age did not influence the extent to which memories were modified or preserved following prediction error. These findings challenge time-dependent consolidation models that forefront memory age as the critical boundary condition for updating and instead suggest that, for complex human episodic memory, memory strength is the more influential factor.

Our demonstration that prediction error selectively updates weak, but not strong, memories clarifies an important boundary condition and constitutes a significant extension of prior work. This stands in contrast to rodent studies, which have found that prediction error was critical for updating strong memories but had little effect on weaker ones [11,32,38–40]. Instead, our results align with the recently proposed EMRC framework [28,45], which posits that strong memory reactivation helps people to detect prediction errors consciously, enabling the formation of a recursive representation that includes the original event, the new event and the experience of change—thereby differentiating old and new content. By contrast, this view holds that weaker memory at reactivation leads to poor change detection and the blurring of old and new content in memory. Emerging empirical work has supported this framework by studying how new, related events are learnt in the context of prediction errors [41–43]. Our findings extend this approach by studying how memory for the original event is influenced by prediction errors. Consistent with this body of work, we find that memory strength leading up to the prediction error is critical, but we differ by showing that strong memory strength at reactivation protects the original memory, whereas prior findings show that it supports new learning [41–43]. Additionally, we show that when prediction errors are experienced in the absence of a strong memory, the original memory is likely to be modified, complementing the same prior work showing that weak memory leads to poor new learning owing to interference. This pattern also aligns with aspects of the nonmonotonic plasticity hypothesis [34,35] by providing additional evidence that strong memories tend to be resistant to updating, whereas weaker memories are less resistant [12,25,32,64,65].

The observed interaction between memory strength and prediction error also helps explain why we did not find the same main effect of prediction error on intrusion details as we reported in our past work [49]. Although our procedure was primarily based on the original paradigm, we made several modifications that probably enhanced memory reactivation, thereby limiting the power of prediction errors to drive updating. For instance, after each video was reactivated in Session 2, participants rated how well they remembered it from Session 1. Adding this retrieval rating was instrumental to investigating a moderating effect of reactivation strength, but explicitly reflecting on target video retrieval during the reactivation session probably enhanced its reactivation in memory. Relatedly, during the interference phase, participants were shown the title of the corresponding target video before viewing the interfering video, which gave them several seconds to retrieve the original memory and prepare to distinguish it from the interfering video that shared the same name. These modifications probably enhanced the retrieval of the original memory and provided opportunities to protect it from interference caused by the semantically related videos [28]. As a result, our design appears to have produced stronger memories overall, as evidenced by fewer intrusions and more correct details compared with the original findings from the paradigm that we adapted [49]. Under these strengthened memory conditions, prediction error no longer exerted a uniformly disruptive effect but instead selectively influenced the subset of weak memories that remained susceptible to updating.

By contrast to the robust effects of memory strength, we found no effect of the memory's age at reactivation on memory updating. Although the delay between encoding and reactivation varied widely (1 h, 24 h or 2 weeks), its manipulation neither influenced any memory outcome measures nor interacted with prediction error. These results directly contrast with those from the rodent literature, which suggest that time-dependent consolidation sets critical boundary conditions on memory modification [6,7,9,11,19]. There are multiple possibilities that could underlie this discrepancy. First, the effect of delay in prior rodent studies may have been confounded with reactivation strength. For example, older rodent memories may require prediction error to update, not because they are more robust but because their (unmeasured) reactivation was weaker than younger memories. Indeed, one study found that strong memories in rodents that were initially resistant to updating became susceptible over time [36], potentially because their effective strength at reactivation declines with forgetting. Since rodent research has focused on manipulating the strength of encoding, rather than measuring the memory strength at reactivation, the concurrent effects of reactivation strength and memory age are yet to be teased apart. By independently measuring memory strength at reactivation and modelling it alongside memory age, the present study was able to separate these influences in humans. Our findings suggest that although memory strength declined with longer delays, memory age itself did not explain additional variance in memory outcomes once memory strength was accounted for.

Another possibility for the cross-species differences is that time-dependent consolidation is less critical for naturalistic memory in humans, at least at the timescales we investigated. For example, neuroimaging studies have revealed that hippocampal engagement during autobiographical memory retrieval is better predicted by the quality of retrieval than the age of the memory, lending support for multiple trace and trace transformation theories of memory consolidation [66–69]. From this perspective, it may not be surprising that only memory strength independently predicted memory updating. Moreover, a recent study in humans using similar delay manipulations to those employed here also failed to replicate rodent findings, showing no effect of temporal spacing between related episodes in terms of integration or differentiation of those memories [70]. Together, these results suggest that temporal delay—a key boundary condition in rodent models—does not appear to constrain the updating of complex human episodic memories.

Importantly, cross-species comparisons should be interpreted in light of fundamental differences in the nature of the memories being studied. Rodent paradigms often involve simpler associative memories with high ecological relevance for survival, whereas the complex, narrative-based episodic memories examined in humans involve richer semantic structure and multiple contextual elements. At the same time, recent rodent work—including the studies referenced here [11,19,32,38,39]—has increasingly moved beyond purely aversive fear conditioning to incorporate novelty and context-based prediction error manipulations that more closely parallel human paradigms. Future research may benefit from continued convergence across species, with animal models incorporating greater event complexity and human studies leveraging more naturalistic, motivationally relevant learning conditions that better capture the adaptive significance of prediction error in real-world memory updating.

Beyond insights into cross-species translation, the minimal impact of delay observed here raises questions about the generalizability of delay effects across stimulus domains within human memory research. In particular, the spaced learning literature has shown that longer intervals between learning sessions enhance later retention [71–74]. Our paradigm resembles a spaced learning design, yet longer intervals between encoding and reactivation (mirroring two spaced learning sessions) had no benefits for subsequent recall. One key distinction lies in the materials used: most spaced learning studies rely on relatively simple stimuli such as word-pair associations, image recognition or classroom-style fact learning, whereas our design employed rich, naturalistic narratives that may carry personal relevance and engage prior knowledge. Memory for these naturalistic stimuli may involve different neural mechanisms, as related prior knowledge provides a supportive schematic structure. Since these sorts of schemas accelerate systems-level consolidation [75–77], the age of the memory may be less related to the physiological mechanisms underpinning spacing effects in our task and real-life experiences.

More broadly, prediction error paradigms themselves vary substantially in both the types of stimuli and the nature of the violations they induce, ranging from changes in learnt associations or sequences between words or images to modified features and endings in narrative events, among other forms [5,30,34,41,78–80]. These paradigms probably differ not only in their memorability, consolidation dynamics and the susceptibility of the original memory to interference, but also in the salience and functional significance of the prediction errors themselves. Naturalistic narrative events, such as those used here, contain rich semantic and schematic scaffolding that may support more durable representations and reduce sensitivity to time-dependent degradation compared with simpler associative or category-learning stimuli [50,76,77,81]. This possibility is consistent with our finding that memory age did not independently predict updating once reactivation strength was considered. Such differences in stimulus domains could influence both how memories consolidate and how readily they are modified following prediction error, potentially contributing to the variability in boundary conditions observed across studies. Differences in the magnitude, timing and relevance of prediction errors across paradigms may further shape whether memories are weakened, updated or protected. Clarifying how stimulus properties and prediction error characteristics jointly shape memory updating remains an important direction for future research.

Two broad classes of mechanisms could account for our memory-updating effects: reconsolidation and memory-competition frameworks. These frameworks differ not in whether updating occurs, but in how this happens: reconsolidation assumes modification of the original trace [1,29,81–85], whereas a memory competition account posits the coexistence of multiple traces whose accessibility varies with retrieval dynamics [28,86–90]. Like the inspiring work of Sinclair and Barense [49], the paradigm on which the current work is based was designed to target reconsolidation mechanisms: interfering content was presented several minutes after reactivation to allow time for synaptic destabilization [91,92], and memory updating following reactivation and interference was assessed after a delay of 24 h to allow for the protein synthesis required to restabilize the memory trace [92–94]. Indeed, this work showed that prediction error-driven updating occurred only under the critical temporal conditions

required for reconsolidation, consistent with a destabilization-and-restabilization process [49]. Since our task is highly similar to this original paradigm, our findings probably suggest that memory strength sets boundary conditions for reconsolidation in humans; the destabilization of weakly reactivated memories in the context of prediction errors leaves them vulnerable to the insertion of related content presented within the reconsolidation window. However, we remain entirely open to the possibility that memory competition also plays a role, as these mechanisms are not mutually exclusive. From this perspective, prediction error may weaken poorly reactivated memories, creating source confusion between the target and interference videos, thereby leading to heightened intrusion rates. Recent evidence supports this possibility, demonstrating that the hippocampal representations of original events can remain intact even while competing with newly formed misinformation traces at retrieval [95]. Reconsolidation and memory competition may represent different routes by which prediction error leads to updating, and teasing them apart is notoriously difficult. Indeed, both mechanisms are consistent with our finding that memories containing more intrusions and errors also contained fewer correct details—a pattern that could reflect reconsolidation-driven replacement of original content or, alternatively, a competitive advantage for the interfering memory trace. Thus, rather than favouring one framework, our results highlight the powerful influence of prediction error in modifying memories.

5. Conclusion

The present study demonstrates that not all memories are equally susceptible to prediction error-driven updating. By independently manipulating memory age and memory strength, we show that strength, not age, determines whether prediction error leads to memory modification. Our findings clarify the boundary conditions of prediction error-driven updating and they bridge theoretical perspectives from animal and human research. For complex episodic memories, the age of memory does not appear to constrain updating as it does in rodent models, suggesting that the time course of consolidation alone cannot explain memory malleability in humans. Rather, subjective memory strength at reactivation—a feature uniquely accessible in human paradigms—emerged here as a more direct determinant of whether memories are modified or preserved. By integrating naturalistic paradigms with subjective and behavioural measures, this work advances our understanding of when and how prediction error shapes the human memory system, offering support for the intuition that not every violated expectation should lead to a memory change. Memory strength limits when prediction error updates a memory, protecting strong, well-established memories from being overwritten by transient surprises while still allowing weak, uncertain memories to be updated. This selectivity helps to maintain an adaptive balance between memory stability and flexibility.

Ethics. This study was approved by the Research Ethics Board at the University of Toronto (Protocol: 55931). Written informed consent was obtained from all participants by the first author and trained research assistants prior to the start of the experiment.

Data accessibility. The data and analysis scripts of this study are available on the Open Science Framework (OSF) at [96]. Memory interview transcripts are not publicly shared because they contain potentially identifying information. De-identified transcripts may be made available upon reasonable request to the corresponding author.

Supplementary material is available online [97].

Declaration of AI use. Grammarly and ChatGPT were used for minor grammatical revisions and phrasing suggestions in the manuscript text. ChatGPT was also used to assist with troubleshooting analysis code. All analyses and final manuscript content were reviewed and verified by the authors.

Authors' contributions. C.M.Y.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, validation, visualization, writing—original draft, writing—review and editing; K.D.: conceptualization, funding acquisition, investigation, methodology, resources, software, supervision, validation, writing—original draft, writing—review and editing; M.D.B.: conceptualization, funding acquisition, investigation, methodology, resources, software, supervision, validation, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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