# Prior knowledge influences the neural mechanisms supporting memory-based inference

## Schema-congruency and memory-based inference

Zhenghao Liu (zhenghao.liu@psy.lu.se), Inês Bramão and Mikael Johansson

Department of Psychology, Lund University, Sweden

**Conflict of interest statement**

The authors declare that there is no conflict of interests.

**Acknowledgements**

This work was supported by the Swedish Research Council Grant VR 2019-02455. We thank Ieva Valavičiūtė for the assistance in data collection and stimuli preparation and all the volunteers who participated in this study.

**Significance Statement:**

To make informed decisions, we often need to combine information from separate events. This study shows that prior knowledge, or schemas, affects how the brain forms these connections to make inferences about the world. Using EEG and machine learning, we found that when new information fits with existing schemas, people usually integrate memories during learning. In contrast, when information conflicts with prior knowledge, successful inference depends on retrieving and merging separate memories at the time of the decision. These findings reveal that the brain can switch between encoding and retrieval strategies based on prior knowledge, providing new insight into how memory supports reasoning, decision-making, and adaptive behavior.

**ABSTRACT**

Memory-based inference allows individuals to integrate information acquired across separate episodes to support novel decisions and reasoning. Although prior knowledge, such as schemas, is known to influence learning and memory, its impact on the neural mechanisms underlying inference remains unclear. In this study, we investigated how schema congruency affects the encoding and retrieval of overlapping events and how these processes contribute to memory-based inference. Thirty-nine participants encoded AB associations, consisting of picture-word pairs presented on either schema-congruent or schema-incongruent backgrounds. These were followed by BC associations involving the same word paired with a new picture on a neutral background. At test, participants were asked to infer the indirect AC association. While overall inference accuracy did not differ as a function of schema congruency, behavioral and neural data revealed distinct mechanisms. Inference for schema-incongruent events depended on accurate retrieval of both AB and BC associations, whereas schema-congruent inferences did not. To investigate the neural processes involved, we trained hierarchical multivariate pattern classifiers on EEG data to detect schema and context reinstatement during task performance. For schema-congruent events, successful inference was predicted by schema reinstatement during BC encoding, consistent with integrating overlapping information into a unified memory trace. In contrast, successful inference for schema-incongruent events was predicted by context reinstatement during AC retrieval, reflecting a reliance on flexible recombination of separate memory representations. These findings demonstrate that schema congruency modulates the neural basis of memory-based inference. Congruent events are integrated during encoding, whereas incongruent events rely on retrieval-based inference.

**Keywords:** memory integration, schema, congruency, context, MVPA, EEG

## INTRODUCTION

Life events often involve overlapping elements such as people, objects, and places. These shared features allow memories to interact and influence how new experiences are encoded in relation to prior knowledge (Schlichting and Preston, 2015). For example, observing one person holding a book in a classroom and later seeing another person with the same book may lead to the inference that they study together. Such memory-based inferences rely on integrating information across separate episodes and can arise through different mechanisms. One possibility is that familiar elements in new experiences trigger the reactivation of related past events, promoting the formation of integrated memory traces that combine old and new information (Eichenbaum, 1999; Shohamy and Wagner, 2008; Zeithamova et al., 2012). Alternatively, to reduce interference, the brain may encode and retrieve overlapping events as distinct representations that preserve their individual episodic details (McClelland et al., 1995; O'Reilly and Rudy, 2000; Kumaran and McClelland, 2012; Kumaran et al., 2016).

While prior knowledge supports learning and memory, it is less clear how it shapes the balance between integration and separation in the service of memory-based inference. In particular, how schema congruency guides how overlapping events are learned and remembered. To address this, we used multivariate pattern analysis (MVPA) of electroencephalographic (EEG) data to track the reactivation of schemata and context-specific information during a memory-based inference task involving congruent and incongruent events.

Schemas are abstract knowledge structures that generalize across experiences by capturing semantic regularities while filtering out perceptual detail (Ghosh and Gilboa, 2014). For instance, although classrooms may differ in appearance, they share the basic function of a learning space. Schemas, mediated by the medial prefrontal cortex (Brod et al., 2015), provide a framework for organizing new information and support both encoding and retrieval (Anderson, 1981; Staresina et al., 2009; Van Kesteren et al., 2020; Audrain and McAndrews, 2022). Importantly, their influence is not limited to congruent information. When new experiences deviate from expectations, memory can be enhanced by prediction error signals (Tulving and Kroll, 1995; Greve et al., 2017; Frank et al., 2018; Ortiz-Tudela et al., 2024), driving the medial temporal lobe, particularly the hippocampus, to encode novel event-specific details and update existing knowledge (Van Kesteren et al., 2013; Greve et al., 2017). This suggests a non-linear relationship between schema congruency and memory (Van

Kesteren et al., 2012), where congruent and incongruent events enhance learning via distinct neural systems.

However, it remains unclear how schema congruency dynamically shapes encoding and retrieval processes to support memory-based inference. To investigate this, we developed a paradigm where participants encoded AB associations—picture-word pairs presented on a contextual background—with schema congruency manipulated by varying the semantic fit between the word and background (e.g., “desk” vs. “corn” with a classroom scene). Participants then encoded overlapping BC associations, pairing the same word with a new picture on a neutral background. At test, we assessed their ability to infer indirect AC associations, as well as memory for AB and BC pairs and the associated schema and context (see **Figure 1A**).

We trained hierarchical classifiers on EEG data from AB encoding to distinguish neural patterns associated with schema and context, then applied these classifiers to BC encoding and AC retrieval (see **Figure 1B**). Because contextual information is reinstated alongside studied content (Diana et al., 2013; Miller et al., 2013; Folkerts et al., 2018; Bramão et al., 2022), we could track how different forms of reactivation support memory-based inference. Schema reinstatement reflects retrieval of semantic knowledge and integration, while context reinstatement reflects retrieval of event-specific details.

We hypothesized that inference for schema-congruent events would be driven by integrative encoding, with schema reinstatement during BC encoding predicting later inference. In contrast, inference for schema-incongruent events would rely more on flexible retrieval, with context reinstatement during AC predicting performance. As shown below, our findings support these predictions, revealing distinct neural mechanisms supporting inference depending on whether new information aligns with prior knowledge.

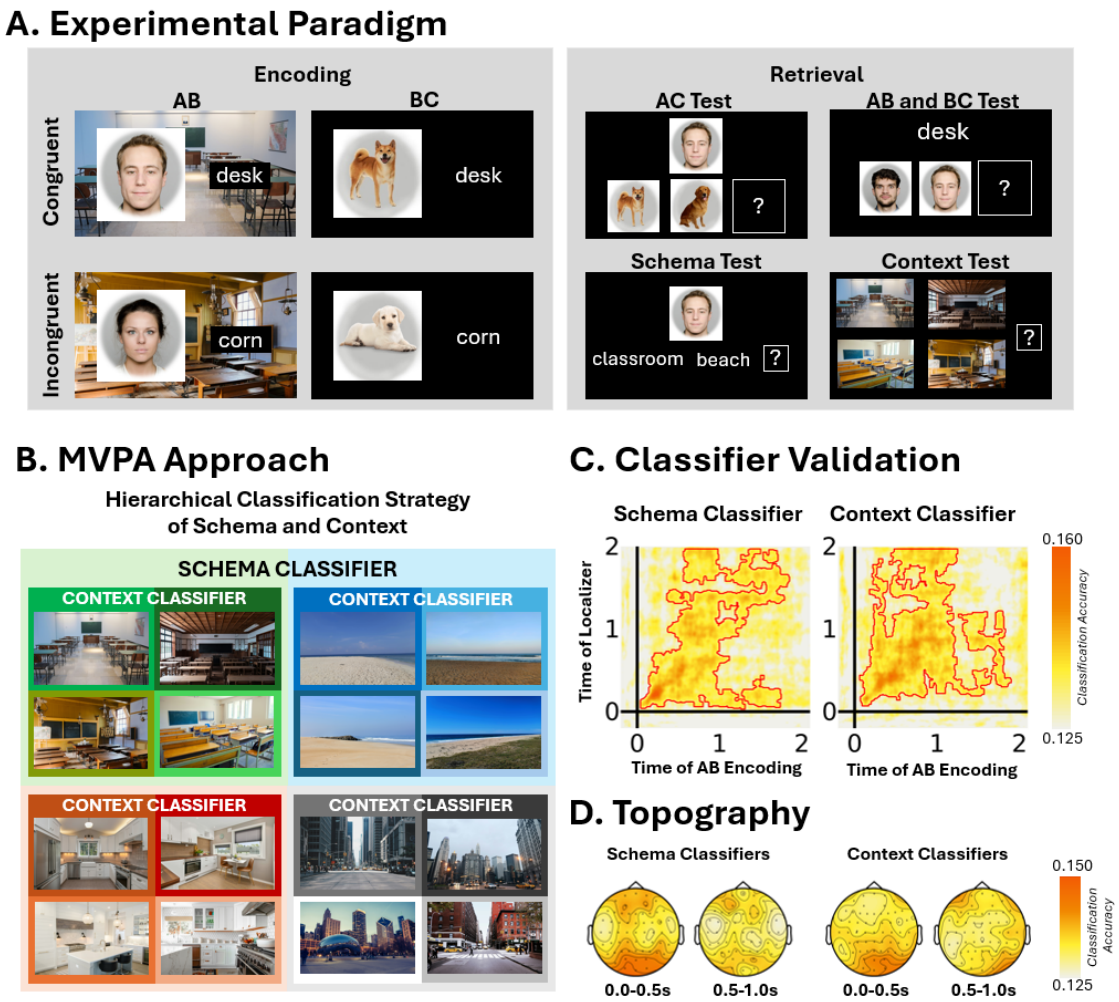


**Figure 1.** Overview of study design and analytical approach. (A) Experimental paradigm. Participants encoded AB and BC events consisting of picture-word pairs presented on either a contextual (AB) or neutral (BC) background. Schema congruency in AB events was determined by the semantic relationship between the word (B) and the contextual background. For BC events, schema congruency was determined by the corresponding AB pair. At retrieval, participants completed memory tests for inferred AC associations, direct associations, and schema/context memory. All tests included an "I don't know" response option to minimize noise from guessing. Face stimuli were selected from the Oslo Face Database (Chelnokova et al., 2014), with individuals having provided consent for publication. Bird and context images were similar to those used in the original experiment, but for illustrative purposes, license-free images were sourced from the Unsplash database (https://unsplash.com/license). (B) Hierarchical classification approach. EEG data recorded during a localizer task were used to train hierarchical multivariate pattern classifiers for schema and context. Schema classification aimed to differentiate between eight semantic categories (beach, farm, forest, city, classroom, bathroom, airport, kitchen), while context classification distinguished between eight unique exemplars within each schema. Context classification accuracy was obtained by averaging

across the eight exemplar classifiers. The figure displays four of the used schemas and four of their context exemplars. (C) Time-generalized classification. Classifiers trained on the localizer data were applied to data recorded during AB encoding, in a time period when only the context was onscreen. Classification accuracy significantly above chance (1/8) is indicated by red contours. Plots were smoothed with a 2D Gaussian kernel (50 ms width) solely for visualization purposes. (D) Channel contribution maps. Topographic plots show the contribution of individual EEG channels to schema and context classification performance.

# METHOD

## Participants

We collected data from a total of 40 participants. Data from one participant was excluded due to excessive noise in the EEG data. Thus, the final sample consisted of 39 participants (average age 29.9 ± 6.4 years, 10 males and 29 females), all with normal or corrected-to-normal vision. All participants were right-handed, fluent in English, and reported no psychiatric or neurological disorders. For their time in the lab (averaging 3 hours per participant including EEG preparation), participants received monetary compensation in the form of vouchers to be used in various shops.

All procedures were carried out in compliance with the Swedish Act concerning the Ethical Review of Research involving Humans (2003:460) and the World Medical Association's Declaration of Helsinki's Code of Ethics. Participants provided their informed written consent before taking part in the study. The data collection was anonymous and did not involve any potentially identifying demographic information. As established by Swedish authorities and specified in the Swedish Act concerning the Ethical Review of Research involving Humans (2003:460), this study does not require specific ethical review by the Swedish Ethical Review Authority due to the following reasons: (1) it does not deal with sensitive personal data, (2) it does not use methods that involve physical intervention, (3) it does not use methods that pose a risk of mental or physical harm, (4) it does not study biological material taken from a living or deceased human that can be traced back to that person.

## Stimuli material

A total of 64 color photos, downloaded from various sources on the internet and resized to 1920 ×1080 pixels, served as background contexts. We used eight different contextual pictures for each schema. Half of the schemas were outdoor (city, forest, beach, and farm) and the other half were indoor (kitchen, airport, bathroom, and classroom).

Additionally, 128 images of human faces (half male and half female) taken from the Oslo Face Database (Chelnokova et al., 2014) and 128 images of dogs downloaded from various sources on the internet were used in the experiment to form picture-word associations. All the dog images were removed from their original backgrounds, resized to 500 × 500

pixels, and placed on a light grey surface in a white background to match with the face stimuli.

A pool of 128 singular concrete nouns was selected from the Small World of Words dataset for English word associations (De Deyne et al., 2019). Specifically, we selected 16 congruent words for each schema according to their association with the schemas. The frequency of the words was checked with the Corpus of Contemporary American English (Davies, 2008). The schema-congruent words were divided into four lists. We tested if the lists were equivalent in terms of association strength with the schema, frequency and length. This was evaluated with the *BayesianFactor* (0.9.12) implemented in R (4.1.2), the Bayesian Factor in favor of the null hypothesis over the alternative hypothesis ($BF_{01}$) was calculated and a criterion of three was adopted (Kass and Raftery, 1995). We confirmed that the lists were matched in terms of association strength ($BF_{01}$ = 22.611), length ($BF_{01}$ = 5.323), and frequency ($BF_{01}$ = 18.822). Each word was randomly paired with a face and a dog to form the AB and the BC associations. For half of the corresponding AB and BC associations, the A was a face, and the C was a dog; the other half was the opposite. Each list was assigned to one experimental condition. The incongruent lists were formed by shuffling the words across the different schemas, ensuring that the words did not fit the schema (e.g., the word ‘fridge’ and ‘baggage’ for the schema of *beach*). To ensure that differences between conditions were not due to differences in the stimuli material, the assignment of the lists to the experimental conditions was counterbalanced across participants.

**Procedure**

The stimuli were presented electronically using the E-Prime 3.0 software (Psychology Software Tools, Inc. [E-Prime Go], 2020) on a 19-in. monitor with a resolution of 1920 ×1080 pixels. The stimuli were presented against a black background. The words appeared in a white rectangular box of 100 × 200 pixels with black bold Arial Unicode MS font and a size of 20.

The session started with the localizer task, in which participants were presented with 64 contextual images corresponding to the eight schemas. The pictures were randomly presented, one at a time and for 2000 milliseconds. Participants were asked to identify whether the contextual picture represented an indoor or outdoor scene by pressing ‘i’ for indoor and ‘o’ for outdoor. Each contextual picture was shown five times. The data acquired

during this localizer task were used to build the multivariate pattern classifiers of schema and context (see **Figure 1B**).

After the localizer task, participants were introduced to the memory task. The task comprised eight blocks, and participants were encouraged to take breaks between blocks. Each block consisted of an encoding phase, a distractor task, and a retrieval phase. In the encoding phase, participants were asked to encode the events, composed of a word and a picture (face/dog) displayed on top of a background (see **Figure 1A**). For AB events, the background are contextual images, which can be either schematically congruent or incongruent with the word B. In contrast, BC events comprise a black background, with their schema congruency inherited from the corresponding AB events. Participants were asked to learn eight AB followed by eight BC. Half of the events were schema-congruent, and the other half were schema-incongruent. In each block, participants encoded congruent and incongruent events of two schemas, each consisting of an indoor and an outdoor environment. The eight schemas were grouped in pairs in the following way: a) beach and classroom, b) city and kitchen, c) forest and airport, and d) farm and bathroom. There were two blocks of each schema pair, and the presentation order of the schema pairs was counterbalanced across participants. Participants were asked to encode all the direct (AB and BC) and inferred associations (AC) and to memorise the context in which the associations were presented. Non-overlapping XY associations were also implemented in the present experiment but were not included in the present analyses. In the retrieval phase, participants were first tested on all the inferred AC associations, followed by the retrieval of the schema and the context in which the picture A appeared. After that, all the direct associations were tested (see **Figure 1A**).

The AB encoding trial started with a fixation cross for 1 second. Next, the contextual picture was displayed for 2 seconds, followed by the word B presented for 1 second on the right side of the screen. After that, the picture of the face/dog was displayed on the left side of the screen and remained, together with the word and the context, for another 5 seconds. The BC trials started with the presentation of the C, for 5 seconds, on the left side of the screen, followed by the presentation of the B for another 5 seconds, on the right side of the screen. Each trial was preceded by a jittered black screen, ranging between 0.25 and 0.75 seconds. At retrieval, the trials started by presenting a fixation cross for 1 second. After that, the cue, picture A, was displayed for 2 seconds. Thereafter, the target, corresponding picture C, and a distractor, a picture Y from a non-overlapping XY association, were presented in the bottom half of the screen and remained for a maximum of 6 seconds. The distractor was presented

during encoding in the same contextual picture and belongs to the same category (dog vs. face) as the target. The AC test was followed by the schema memory test, in which participants indicated the schema where the A was originally presented (schema memory test). If answered correctly, participants were to indicate in which one of the four contexts it was presented (context memory test). Participants were given the option to press the "I don't know" in case they did not remember. This was added to decrease the noise of the guessing responses.

**EEG data collection and preprocessing**

A SynAmps RT Neuroscan amplifier (1 kHz sampling rate; left mastoid reference; bandwidth DC-3500 Hz; 24-bit resolution) with 62 active electrodes mounted in an elastic cap was used to collect EEG data. The electrodes were positioned according to the extended 10-20 system. Additional electrodes were used for references (left and right mastoids), virtual ground (placed between Fpz and Fz), and vertical electrooculogram (EOG, placed in the cheek, below the right eye). The EEG data were preprocessed using FieldTrip (Oostenveld et al., 2011) and in-house MATLAB scripts. Offline, the EEG data was down-sampled to 500 Hz. A lowpass (up to 100 Hz) and a notch filter (50 and 100 Hz) were applied to the data to extract the frequency of interest and remove common noise of alternating current.

Afterwards, the data was clipped into epochs. The data from the localizer task were used to build the hierarchical schema and context classifiers. These data were epoched from -1 to 3 s relative to the onset of the contextual picture. The AB encoding epochs, used to validate the schema and context classifiers, ranged from -1 to 3 seconds relative to the onset of the first context picture. The BC encoding epochs ranged from -1 to 5 seconds relative to the onset of the BC association. The AC inference test epochs ranged from -1 to 3 seconds relative to the onset of the cue, which included the time when the target and distractor were also presented for 1 second. The epoched data was transformed into a link-mastoid reference and demeaned (by subtracting the average amplitude of the whole epoch). Additional electrooculogram measures were estimated using the Fp2 electrode and the electrode below the right eye, and the FT7 and FT8 electrodes in the cap to detect vertical (blinks) and horizontal eye movements.

The epochs were visually inspected to remove those with artifacts other than excessive muscle activities, blinks, and eye movements. Independent component analysis was

conducted to remove the components representing oculomotor artifacts and muscle activities that were distinct from the EEG signal. In addition to all the above, bad channels were identified before the whole preprocessing and were interpolated before analysis. Finally, the data were again visually inspected to remove trials containing remaining artefacts.

The final analysis included an average of 311 familiarization trials (ranging between 292 and 319 trials), 59 AB trials (ranging between 51 and 64 trials), 61 BC trials (ranging between 57 and 64 trials) per participant. The data at the inference test contained on average 60 AC test trials (ranging between 58 and 63 trials).

**Behavioral data analysis**

The behavioral data were analyzed with linear mixed models using R (4.1.2) packages of *lme4* (1.1-34) and *emmeans* (1.8.7) for model fitting and statistical tests and *effectsize* (0.8.9) for effect size estimation. The first level of each model was the trial level, which was clustered in the second level, i.e., the participant level. The significance criterion of $p < .05$ was applied for all statistical analyses. Trials in which participants did not respond within the given time frame or responded “I don’t know” were considered incorrect.

First, behavioral performance for the AC inference test and the direct associations was contrasted in terms of accuracy and response times (RTs). Linear mixed models were fitted with the factors Association Type (AC vs. AB vs. BC) and Congruency (Congruent vs. Incongruent). Then, we tested the reliance of the AC inference on the joint accuracy of AB and BC associations to infer the mechanism behind memory integration across schema-congruent and incongruent events. If AC inference was made by integrating AB and BC memories during encoding, then AC inference should not show reliance on the joint AB and BC accuracy at the test phase. On the other hand, if AC inference is accomplished via flexibly retrieving AB and BC at the time of test, then the joint accuracy of AB and BC should predict AC inference performance. To test this, linear mixed models were built using the joint accuracy of AB and BC associations to predict the corresponding AC accuracy. The accuracies of AB and BC associations were included as controlled variables. Two models were built separately for schema-congruent and incongruent events.

Next, memory for schema and context was examined. The accuracy of schema memory was calculated based on all trials; however, for the context memory analysis, only correct schema memory trials were included. Linear mixed models were performed with the

factors of Congruency (Congruent vs. Incongruent) and AC accuracy (correct vs. incorrect) to estimate how schema congruency and inference affect memory for schema and context.

The normality of the residuals model was assessed by inspecting the Q-Q plots of the standardized residuals and Shapiro-Wilk's tests. The homogeneity of variance of the model residuals was assessed for each model by visually inspecting a plot of the model residuals versus fitted values and using Levene's test for unequal variance. Significant complex effects were followed up with post hoc tests with Tucky-correction. Effect sizes, partial eta squared ($\eta_p^2$) for F-tests and unstandardized difference (*D*) for t-tests, were also reported together with other statistics.

**Schema and context multivariate pattern classification**

The multivariate pattern classification was implemented with the MVPA-light package (Treder, 2020) and in-house MATLAB scripts. The multiclass linear discriminant analysis was used to classify the amplitudes of the EEG signal into different schemas and contexts. The classification at the schema level aimed at classifying the EEG amplitudes into eight different schemas (i.e., beach *vs*. farm *vs*. forest *vs*. city *vs*. classroom *vs.* bathroom *vs.* airport *vs.* kitchen), while the classification at the context level aimed at classifying the EEG amplitudes into eight different exemplars (contexts) within each schema (see **Figure 1B**). The pattern classifiers were trained with the data collected during the localizer task, which included the EEG waveforms associated with viewing each picture five times.

Prior to classification, the EEG waveforms were down-sampled to 100Hz and smoothed with a 0.1s moving window to reduce redundancy in classification features and speed up computations. After that, each epoch was baseline corrected by subtracting the averaged amplitude between -0.2 and 0s for each channel. Finally, the EEG amplitudes were z-scored across trials. Classifiers were built at each time point of the EEG waveform, between -0.2s to 2s with respect to the onset of the contextual picture and tested on each time point of AB encoding trials to validate the classifiers (see **Figure 1C**), resulting in a time-generalized classification matrix of 221 × 221 time points. The time-generalized classification matrices for all eight context classifiers were averaged to get the accuracy of the context classification for each participant.

To investigate the neural substrate of schema and context classification, we examined the channel contribution to schema and context classification. We trained classifiers to

distinguish schema and context using the localizer data of each channel and their neighboring channels at each time point (Bramão and Johansson, 2018), which was tested with the same channels at the same time point of the AB data. This procedure resulted in a time course of accuracy estimation for each channel, showing how each channel contributes to the classification of schema and context as a function of time. The topography of the channel contribution is summarized in **Figure 1D**.

Next, the schema and context classifiers were tested on all time points during BC encoding and during AC test to investigate schema and context reinstatement, resulting in time-generalization matrix of 221 × 521 for BC encoding data and 221 × 221 for AC inference test data). The time-generalized classification matrices for all eight context classifiers were averaged to get the accuracy of the context classification for each participant.

**Statistical analysis of the multivariate pattern classification**

To reduce the impact of multiple comparison issue in classic statistics, the statistical significance of the classification accuracy was tested with Bayesian statistics using a Gamma distribution prior (alpha = 30, beta = 210) that accounts for potential false discoveries by applying constraints in prior expectation and precision (Han, 2020; Bramão et al., 2025). For the validation with AB encoding trials, the overall results were obtained by accumulating the accuracy of each participant with consecutive Bayesian update, and the posterior was contrasted against chance (1/8). For the schema and context reinstatement capture in BC encoding and AC test trials, the classification accuracies were contrasted between trials with correct AC inference versus trials with incorrect AC inference (Pham-Gia et al., 1993), to identify schema and context reinstatement that contributed to AC inference. To give further support to our interpretations, we also tested schema and context reinstatement separately for AC correct and for AC incorrect trials. In this case, the obtained classification was contrasted against chance (1/8). The overall results estimation across participants was also done by accumulating the differences of each participant with consecutive Bayesian updates. The final posterior distribution was compared against 0. For all time-generalized analysis, the Bayesian Factor in favour of alternative hypothesis ($BF_{10}$) > 3 (Kass and Raftery, 1995) was adopted as the indicator of the significance. Only significant results lasting for at least 150 ms are reported to avoid spurious findings. For visualization purposes, classification result plots were smoothed using a 2D Gaussian kernel (50 ms width). Importantly, smoothing was not used when evaluating the statistical significance of the effects or when reporting the results.

Given our predictions that memory integration for schema-congruent and incongruent events is supported by different mechanisms, the statistical tests of the EEG data were performed separately for schema congruent and incongruent trials.

**Relationship between schema and context reinstatement and memory**

Upon identifying time windows of schema and context reinstatement during BC encoding and AC test, we further investigated whether they indicate different processes or reflect different aspects of the same process by evaluating their cooccurrence in the trials with correct AC inference. If they tend to co-occur in the same trials, i.e., show significant positive correlation on a trial basis, they are more likely to reflect different aspects of the same process; if they tend to be observed in different trials, i.e., show significant negative correlation on a trial basis, then they might indicate different, complementary processes that jointly lead to successful AC inference. Bayesian linear regression with an Inverse-Gamma-Normal distribution prior (alpha = 15, beta = 15, mu = 0, lambda = 30 * *I*, *I* is unit matrix) with the trial level data was used in this analysis, and the results for all participants were obtained by consecutive Bayesian updates. The standardized regression coefficient was evaluated to reduce the influences of individual differences, the posterior of which was contrast against 0, and the $BF_{10} > 3$ was also adopted as the indication of significance.

Further, to evaluate the potential influence of schema and context reinstatement on schema and context memory, we used the schema and context reinstatement to predict the behavioral performance of schema and context memory tests, using Bayesian linear regression and the data at trial level. The prior, procedure and statistical criteria were the same as above.

# RESULTS

## Associative memory performance

To investigate the impact of schema congruency, we compared memory performance for all associations (AC vs. AB vs. BC) based on whether they were congruent or incongruent with the schema. However, no main effect of Congruency was found in terms of either accuracy ($F(1,7368) = 0.424$, $p = .515$, $\eta_p^2 = 5.76\text{e-}5$) or response times ($F(1,4549) = 0.926$, $p = .336$, $\eta_p^2 = 2.04\text{e-}4$). Instead, we found a main effect of Association Type both on the accuracy ($F(2,38) = 155.614$, $p < .001$, $\eta_p^2 = 0.89$) and the response times ($F(2,38) = 146.968$, $p < .001$, $\eta_p^2 = 0.89$), showing that participants were worse and slower at retrieving AC indirect associations compared with direct AB and BC associations (all *p*s < .001). Additionally, AB associations were retrieved more accurately and faster than BC associations (all *p*s < .001).

The interaction term was significant for accuracy ($F(2,7368) = 3.295$, $p = .037$, $\eta_p^2 = 8.94\text{e-}4$) but not for response times ($F(2,4543) = 1.068$, $p = .344$, $\eta_p^2 = 4.70\text{e-}4$). The interaction showed that schema-congruent BC associations were retrieved less accurately than schema-incongruent BC associations ($t(7368) = -2.392$, $p = .017$, $D = 0.043$), whereas memory performance for all the other associations was not affected by schema congruency (all *p*s > .259; See **Figure 2**).

An exploratory analysis tested the reliance of AC inference on the joint accuracy of AB and BC associations at the test phase. If AC inference was based on the integration of AB and BC during encoding, AC inference should not show reliance on the joint accuracy of AB and BC. However, if AB and BC are flexibly retrieved to support the AC inference, their joint accuracy should be predictive of the AC inference. We observed that for schema-congruent events the joint accuracy of AB and BC was not related to AC performance ($F(1,1240) = 1.498$, $p = .221$, $\eta_p^2 = 4.54\text{e-}3$). However, the joint accuracy of AB and BC was predictive of AC inference for schema-incongruent events ($F(1,1233) = 5.204$, $p = .023$, $\eta_p^2 = 1.21\text{e-}3$).

In sum, no effect of schema congruency was found on AC inference performance, implying that participants are equally capable of inferring across schema-congruent and schema-incongruent events. However, our data indicated that AC inference in these two different conditions is supported by different mechanisms. Specifically, the joint accuracy of AB and BC did not predict AC inference for schema-congruent events, providing no evidence that AC inference relies on the accurate retrieval of AB and BC. In contrast, AC inference for

schema-incongruent events was influenced by the joint AB and BC accuracy, suggesting that AC inference depends on reliable retrieval and recombination of the AB and BC events.

**Schema and context memory performance**

Next, we contrasted schema and context memory as a function of Congruency and AC Performance. An effect of Congruency was found for both schema ($F(1, 2456) = 4.412$, $p = .036$, $\eta_p^2 = 1.79\text{e-}3$) and context ($F(1, 1580) = 117.011$, $p < .001$, $\eta_p^2 = 0.07$), showing higher schema and context memory for schema-congruent compared with schema-incongruent events. An effect of AC performance was found for schema ($F(1, 2495) = 86.783$, $p < .001$, $\eta_p^2 = 0.03$), but not for context memory ($F(1, 1580) = 3.217$, $p = .073$, $\eta_p^2 = 2.03\text{e-}3$). This effect showed that schema memory was higher when AC inference was correct than when it was incorrect.

Additionally, a significant interaction between the two factors was found for both the schema ($F(1, 2469) = 5.5729$, $p = .018$, $\eta_p^2 = 2.25\text{e-}3$) and the context memory ($F(1, 1580) = 9.6767$, $p = .002$, $\eta_p^2 = 6.09\text{e-}3$). For schema memory, the post hoc tests showed that when AC inference was incorrect, schema memory was better when it was congruent compared with when it was incongruent ($t(2466) = 3.328$, $p = .001$, $D = 0.082$), however, when AC inference was correct, no congruency effect was observed ($t(2467) = -0.184$, $p = .854$, $D = -0.005$). On the other hand, context memory for congruent events was higher for AC correct events compared with AC incorrect ($t(1559) = 3.526$, $p < .001$, $D = 0.099$). No differences of context memory were observed for incongruent events ($t(1551) = -0.910$, $p = .363$, $D = -0.027$; see **Figure 2**).

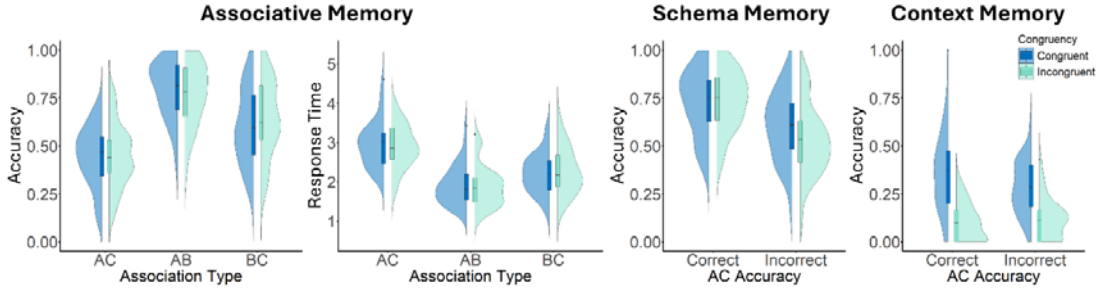


**Figure 2.** Summary of behavioral results for associative memory, schema memory and context memory. For the accuracy and response time of the associative memory test, the data is plotted by Association Type (AC vs. AB vs. BC) and further split by Congruency (Congruent vs. Incongruent).

For schema and context memory, the data is plotted by AC accuracy (Correct vs. Incorrect) and further split by Congruency (Congruent vs. Incongruent). Note that context memory was only tested when participants had made the correct schema choice. Rain cloud plots depict the sample distribution, and the boxplots show the mean, and quartile of the data.

**Hierarchical multivariate pattern classifiers of schema and context**

Multivariate pattern classifiers were trained with the EEG data recorded during the localizer task to capture schema- and context-specific neural activity. These classifiers were trained during the localizer task and validated during AB encoding, in a time window where participants were displayed with the background context only, before being presented with the picture-word associations. This resulted in two different time-generalization maps: one for schema and another for context (see **Figure 1C**). The diagonal of the maps shows the temporal alignment of the training and the test data, indicating that a representation in the training data occurred at the same time point in the test data. On the other hand, the representation captured deviating from the diagonal shows temporal displacement, indicating that a representation in the training data occurred at another time point in the test data (King and Dehaene, 2014). The schema classifiers trained with data ranging between 0.1-1.9 seconds in the localizer task captured the diagonal representations. Those are blended with the representations deviating from the diagonal, captured by the classifiers ranging between 0.8-2.0 seconds. For the context classifiers, the diagonal pattern was captured by the classifiers between 0.1-1.3 seconds, while the diagonal deviating pattern was also captured by the classifiers between 0.8-2.0 seconds. On average, the accuracy of the schema classifiers, showing above-chance classification and marked with the red contour in **Figure 1C** is .140 ($BF_{10}$s > 3.011). For the context classifier the averaged classification is also .140 ($BF_{10}$s > 3.011).

To investigate the neural substrate contributing to schema and context classification, we examined the channel contribution to the schema and context classification (see also Bramão & Johansson, 2018), see **Figure 2D**. These results indicate two distinct patterns of classification: schema classification, as expected (Ghosh and Gilboa, 2014; Gilboa and Marlatte, 2017) involving a frontal component, whereas context classification primarily relies on amplitude differences over posterior channels.

**Schema and context reinstatements for schema-congruent events**

We used the validated classifiers to detect schema and context reinstatement during BC encoding and AC retrieval for schema-congruent events. During BC encoding, the overlapping word (B) was expected to trigger reinstatement of the previously encoded AB episode. We hypothesized that the relative strength of schema versus context reinstatement would influence how the new BC event was encoded in relation to the prior AB. Specifically, because schemas provide a structured framework for organizing information, we predicted that schema-congruent events would elicit reinstatement of the schema context in which the AB association was embedded. This reinstatement was expected to promote integrative encoding, resulting in a unified memory representation encompassing the ABC elements within the relevant schema. At retrieval, this integrated representation would be reinstated to support successful AC inference. To assess these predictions, we compared schema and context reinstatement between trials with correct versus incorrect AC inference.

Following our predictions, during BC encoding, schema reinstatement associated with AC performance was observed in three time windows: 0.0-0.8 seconds (accuracy difference = 0.035, $BF_{10}$s > 3.013), 2.5-3.1 seconds (accuracy difference = 0.037, $BF_{10}$s > 3.012) and 3.2-4.0 seconds (accuracy difference = 0.038, $BF_{10}$s > 3.012) after the onset of the shared word B (see **Figure 3**). Additionally, we also observed context reinstatement associated with AC performance emerging later in the encoding trial, between 3.3-3.6 seconds (accuracy difference = 0.040, $BF_{10}$s > 3.003; see **Figure 3**).

During the retrieval phase, we expected to observe early schema reinstatement, supporting the retrieval of the integrated representation. However, the schema reinstatement was observed later during the retrieval trial, between 2.6-2.9 seconds, in a time window where cue, target and distractor were displayed all on the screen (accuracy difference = 0.038, $BF_{10}$s > 3.001; see **Figure 3**).

After identifying the time windows of significant schema and context reinstatement associated with AC inference, we tested their cooccurrence within the same trials. If they tend to co-occur, they may reflect different facets of the same process; if they occur in different trials, they likely reflect different processes. This analysis was restricted to trials with correct AC inference. First, we assessed the relationship between the different schema reinstatements observed during BC encoding. The early schema reinstatement predicted the late reinstatement at 2.5-3.1 seconds ($\beta$ = .233, $BF_{10}$ = 7.855e+5), and both the early and the 2.5-

3.1 seconds reinstatement predicted the final reinstatement at 3.2-4.0s (early reinstatement: $\beta$ = .133, $BF_{10}$ = 314.956, reinstatement between 2.5-3.1 seconds: $\beta$ = .458, $BF_{10}$ = 1.787e+26). Next, we explored the link between schema reinstatement during BC encoding and both context reinstatement in BC encoding and schema reinstatement during AC test. Early schema reinstatement negatively predicted context reinstatement during BC encoding ($\beta$ = -.092, $BF_{10}$ = 7.738), while the schema reinstatement at 2.5-3.1s negatively predicted schema reinstatement at AC test ($\beta$ = -.078, $BF_{10}$ = 4.504). The complete path diagram is shown in **Figure 4A**. Additionally, schema reinstatement at 2.5-3.1s was related with schema memory ($\beta$ = .054, $BF_{10}$ = 4.446). None of the significant reinstatements predicted schema or context memory ($BF_{10}$s < 2.829).

In summary, our findings reveal sustained schema reinstatement throughout the BC encoding period. This pattern suggests that reactivating the congruent AB schema during encoding likely supported the formation of an integrated memory representation encompassing the ABC elements, which could later facilitate inference. Notably, in trials where early schema reinstatement was absent, successful inference was instead associated with context reinstatement emerging later in the encoding window. This indicates that contextual episodic details can also contribute to the formation of integrated memory representations, potentially through a different pathway.

Unexpectedly, schema reinstatement during the AC retrieval phase was negatively correlated with schema reinstatement during BC encoding. This finding suggests that schema activation at test does not simply reflect the reinstatement of a previously integrated representation. Instead, in cases where early schema activation during encoding did not lead to sustained reinstatement—and an integrated memory was likely not formed—schema reinstatement during retrieval may have supported inference by facilitating the flexible recombination of distinct memory traces.

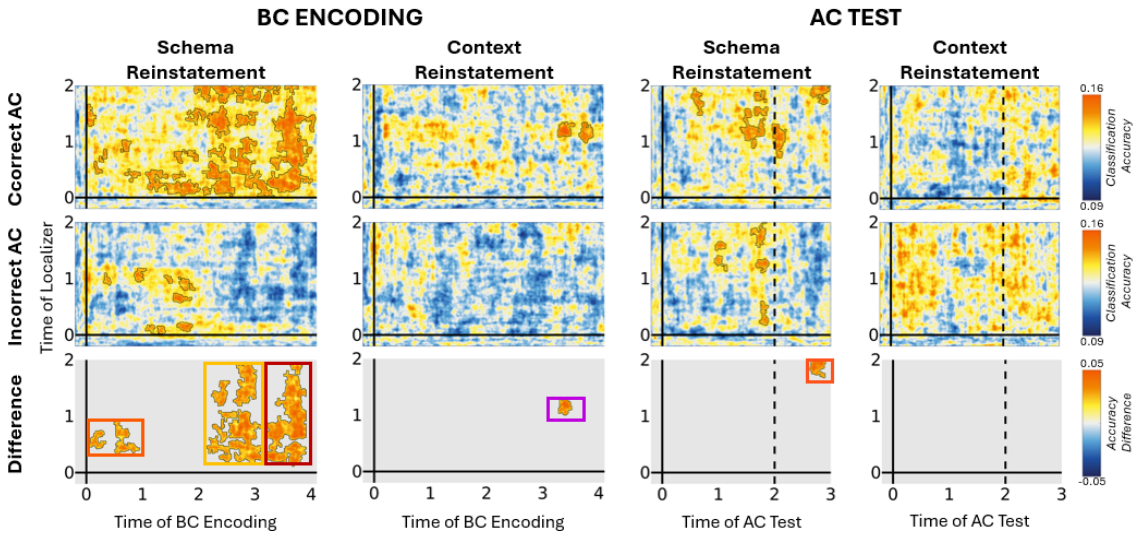


**Figure 3.** Schema and context reinstatement during BC encoding and AC test for schema-congruent events. Trials associated with correct and incorrect AC inference were plotted separately in the top and middle rows, areas with classification accuracy significantly different from chance level were marked with black contours. The bottom row shows the areas with significant differences between trials associated with correct and incorrect AC inference. The dashed line in the time-generalized matrices for the AC test marks the onset of the simultaneous presentation of the cue, target, and distractor. Plots were smoothed with a 2D Gaussian kernel (50 ms width) solely for visualization purposes.

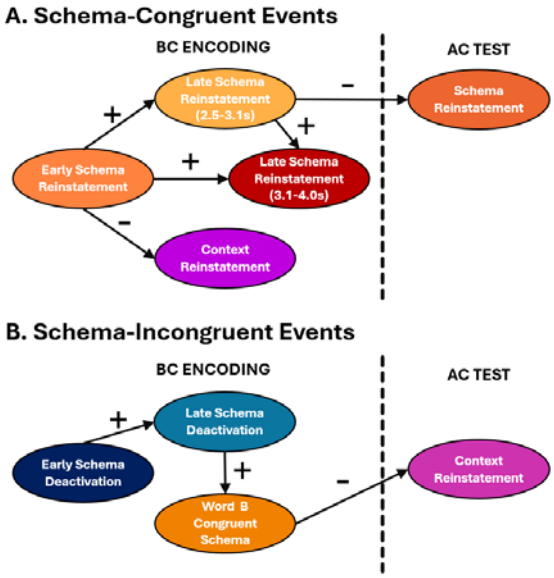


**Figure 4.** The co-occurrence analysis of schema and context reinstatement associated with AC inference, detected during BC encoding and AC test, for the schema-congruent (A) and schema-

incongruent (B) events. Only trials with correct AC inference were included in this analysis. All the relations were estimated at the trial level. Only significant relations are plotted.

**Schema and context reinstatement for schema-incongruent events**

Next, we applied the schema and context classifiers during BC encoding and AC retrieval for schema-incongruent events. Given the lack of alignment between these events and prior knowledge, we did not expect schema reinstatement. Instead, during BC encoding, we predicted reactivation of context-specific information associated with the prior AB event. Because these events lack an overarching schematic framework, they were unlikely to be integrated into a unified representation and were instead expected to be encoded as separate memory traces. Consequently, we hypothesized that successful AC inference would be supported by context reinstatement at retrieval, reflecting the flexible recombination of the distinct AB and BC episodes.

Surprisingly, our results showed, during BC encoding, deactivation of the encoded incongruent schema in two-time windows, at around 1.1-1.8s (accuracy difference = -0.036, $BF_{10}$s > 3.032) and later, at around 2.4-3.1s (accuracy difference = -0.035, $BF_{10}$s > 3.020) after the onset of the shared word B. No context reinstatement was observed during BC encoding (see **Figure 5**).

To shed light on the observed schema deactivations, we analyzed classifier outputs to test whether such deactivation reflected the reinstatement of another schema. Specifically, we examined whether the schema congruent with word B, or the complementary schema co-occurring in the same encoding block, was reinstated when this incongruent schema was deactivated. For this, we extracted the classifier predictions across trials and participants within the areas of significant schema deactivation and calculated the proportion of the labels of these schemas among all labels (i.e., frequency of occurrence). Additionally, the proportion of other non-target schemas were averaged and used as baseline (see **Figure 6A**). The right tail Bayesian *t*-test was adopted to examine if any target schema was detected more frequently than the baseline schemas in trials with correct AC inference. The results showed that, in the late time window, the schema congruent with the word B was more frequently detected (rate difference = 0.022, $BF_{10}$ = 11.973), suggesting that the late deactivation of the encoded incongruent schema relates to the reinstatement of the schema congruent with the word B. Based on this finding, we then evaluated how this reinstatement relates to AC

inference performance (see **Figure 6B**). The results show that reinstatement was higher for AC correct trials compared with AC incorrect trials (accuracy difference = 0.037, $BF_{10}$s > 3.015).

Subsequently, the classifiers were applied during AC test. As expected, we observed significant context reinstatement predictive of AC inference, emerging around 2.6-2.8 seconds, in a time window where cue, target and the distractor were all displayed on screen (accuracy difference = 0.036, $BF_{10}$s > 3.024). This likely reflects the reinstatement of the AB event, necessary for the AC inference, and supporting the flexible retrieval of schema-incongruent events. No schema reinstatement, predictive of AC inference, was observed during AC test (see **Figure 5**).

Finally, we explored the relationship between these schema and context reinstatements in trials with correct AC inference (see **Figure 4B**). We observed that the early incongruent schema deactivation was predictive of the later one ($\beta$ = .392, $BF_{10}$ = 2.694e+19), and that the late incongruent schema deactivation was associated with the reinstatement of the schema congruent with the word B ($\beta$ = -.102, $BF_{10}$ = 16.017). Additionally, the reinstatement of the schema congruent with the word B was negatively related to context reinstatement during AC test ($\beta$ = -.065, $BF_{10}$ = 3.136), indicating that they signal different but complementary processes.

Further, we tested whether the reinstatements of schema and context were predictive of schema and context memory. The results showed that context reinstatement during AC test was negatively related to context memory ($\beta$ = -.050, $BF_{10}$ = 5.120). No other effects were observed ($BF_{10}$s < 1.062).

In line with our hypothesis, context reinstatement during the AC test predicted inference accuracy for schema-incongruent events, reflecting the flexible retrieval and recombination of distinct memory traces that support inference across these episodes. Moreover, context reinstatement was negatively associated with memory for the original context, suggesting that drawing inferences across schema-incongruent events may come at the cost of retaining episodic details from the individual events.

Interestingly, we also observed reinstatement of an event-congruent schema during BC encoding, particularly in trials that were associated with correct inference and low context reinstatement during the AC test. This finding suggests that, in some cases, reinstating a

relevant schema during encoding may support the integration of overlapping events, thereby facilitating later inference.

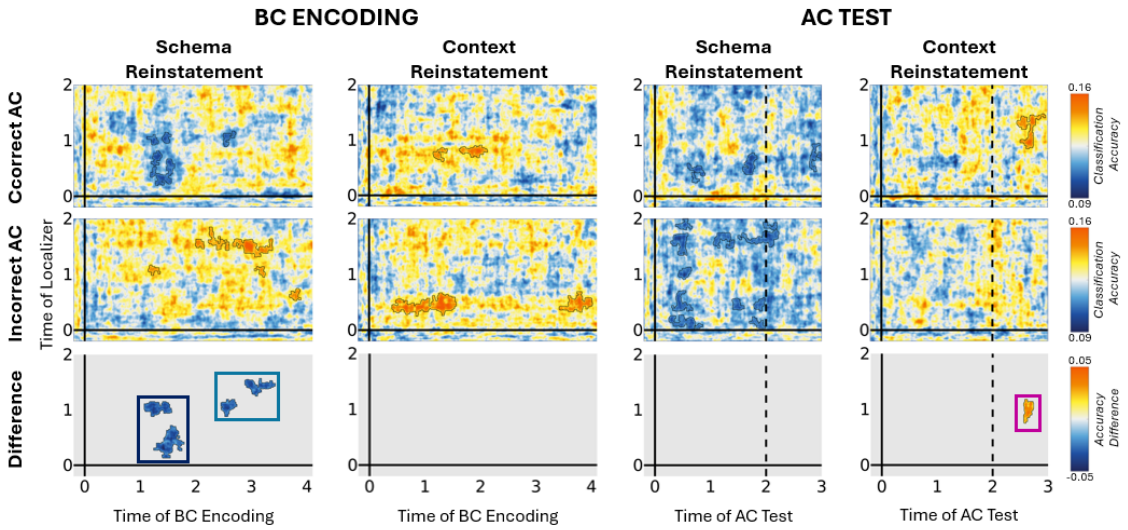


**Figure 5.** Schema and context reinstatement during BC encoding and AC test for schema-incongruent events. Trials associated with correct and incorrect AC inference were plotted separately in the top and middle rows, areas with classification accuracy significantly different from chance level were marked with black contours. The bottom row shows the areas with significant differences between trials associated with correct and incorrect AC inference. The dashed line in the time-generalized matrices for the AC test marks the onset of the simultaneous presentation of the cue, target, and distractor. Plots were smoothed with a 2D Gaussian kernel (50□ms width) solely for visualization purposes.

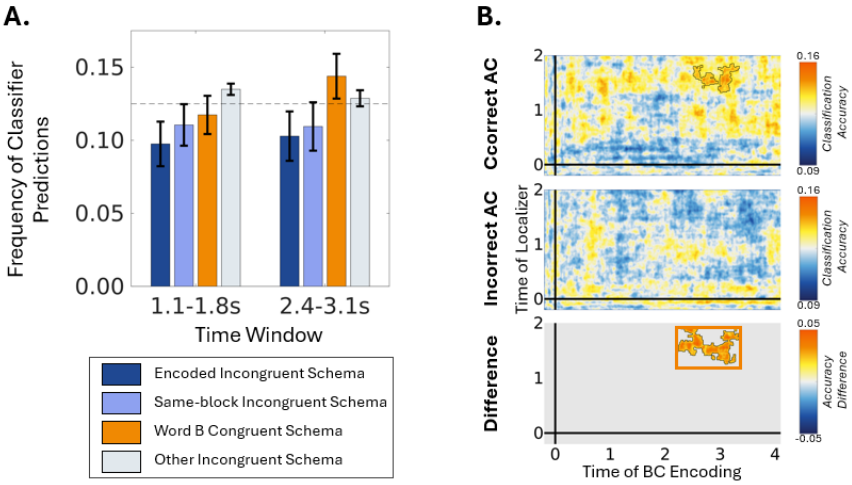

**Figure 6.** Detection of the reinstatement of another schema. (A) Schema classifier output for encoded incongruent schema, same-block incongruent schema, word B congruent schema and all the other incongruent schemas. (B) Reinstatement of the word B congruent schema during BC encoding that contributes to the AC inference across schema-incongruent events. Plots were smoothed with a 2D Gaussian kernel (50 ms width) solely for visualization purposes.

# DISCUSSION

This study examines how schema congruency influences the mechanisms underlying memory-based inference. Participants completed an associative inference task with events that were either congruent or incongruent with pre-existing schemas (**Figure 1**). Although schema congruency did not affect overall inference performance (**Figure 2**), further analysis revealed a key dissociation: AC inference for schema-congruent events was independent of successful AB and BC retrieval, whereas inference for schema-incongruent events relied on the successful retrieval of both. These findings suggest that congruent and incongruent inferences engage distinct memory mechanisms.

To elucidate the mechanisms underlying memory-based inference as a function of schema congruency, we examined the interplay between schema and context reinstatement during task performance, using multivariate pattern analysis (MVPA) of electroencephalography (EEG) data. Given that schemas are structured frameworks that episodic experiences (Anderson, 1981; Staresina et al., 2009; Van Kesteren et al., 2020; Audrain and McAndrews, 2022), we hypothesized that schema reinstatement would promote the formation of integrated representations for schema-congruent events. These integrated representations would support novel inferences across congruent events (Eichenbaum, 1999; Shohamy and Wagner, 2008; Zeithamova and Preston, 2010; Zeithamova et al., 2012; Schlichting and Preston, 2014, 2015). In contrast, when novel experiences deviate from existing knowledge structures, schema-incongruent events are more likely to be encoded as distinct memory traces containing vivid episodic details (Greve et al., 2017). Consequently, inference across these events should rely on flexible retrieval and recombination of these distinct memory traces as needed (McClelland et al., 1995; O'Reilly and Rudy, 2000; Kumaran and McClelland, 2012; Kumaran et al., 2016). Accordingly, we predicted that context reinstatement during the AC test would reflect the retrieval and recombination of distinct memory traces for schema-incongruent events, enabling successful inference.

As predicted, schema-congruent events elicited sustained schema reinstatement during BC encoding, predictive of later successful AC inference. This finding aligns with prior research showing that schema-congruent information benefits episodic memory by providing an organizing framework and is encoded into converging neural representations (Audrain and McAndrews, 2022). Our results extend this work by demonstrating that schema reinstatement during the encoding of overlapping events facilitates the formation of integrated memory representations, which in turn support inference across indirectly related

(AC) event pairs (**Figure 3**). Additionally, schema reinstatement during BC encoding was associated with improved schema memory at retrieval, suggesting a reciprocal relationship: while schemas enhance the encoding of congruent events, the reactivation of event content also strengthens memory for the schema itself. This finding is consistent with evidence that schema representations can be rapidly formed and remain stable over time, particularly when aligned with incoming information (Tompary et al., 2020; Audrain and McAndrews, 2022). Together, these findings support the view that schema-based memory integration is driven by early reactivation of prior knowledge during encoding, which scaffolds the incorporation of new experiences into existing knowledge structures.

Successful memory-based inference for schema-congruent events was also associated with schema reinstatement during the AC test. This reinstatement may reflect different underlying processes. It could indicate retrieval of an integrated ABC representation embedded within the schema or, alternatively, the flexible retrieval and recombination of AB and BC events. If the former were true, we would expect a positive correlation between schema reinstatement during AC retrieval and during BC encoding, as both would reflect access to the same integrated memory trace. However, we observed a negative correlation between schema reinstatement at test and during BC encoding. This suggests that when an integrated representation is not formed during encoding, the schema may be reactivated at retrieval to support the flexible recombination of separate episodes (**Figure 4A**). Conversely, when an integrated ABC memory is available, schema reactivation at retrieval may not be necessary to support inference.

Finally, AC inference for congruent events was also associated with context reinstatement observed during BC encoding. This effect was negatively correlated with schema reinstatement during BC encoding (**Figure 4A**), suggesting an alternative route to forming unified memory representations supported by event-specific contextual information. Particularly, when schema retrieval is absent in the early time window, later context reinstatement may compensate to support the subsequent AC inference. These findings point to the existence of a secondary pathway for memory integration, one that relies on context rather than abstract schematic knowledge. While schema-supported integration likely reflects the activation of generalized knowledge structures that scaffold the assimilation of new information, context-supported integration may depend more heavily on the retrieval of unique episodic details. Speculatively, these two pathways may rely on distinct cognitive and neural mechanisms.

Overall, these findings suggest that AC inference for schema-congruent events is primarily supported by encoding-related mechanisms, with schema reinstatement playing a central role in forming a unified memory representation that links new and prior information. However, when schema reinstatement fails to occur during the encoding of overlapping events, alternative pathways – such as schema reinstatement at retrieval or context-based integration – may be engaged to support successful inference. This highlights the adaptive nature of memory, showing how it dynamically adjusts to varying levels of congruency and the availability of prior knowledge during learning.

Successful AC inference for schema-incongruent events was associated with context reinstatement during test (**Figure 5**). Because these events do not align with pre-existing knowledge structures, they are less likely to be integrated within a schema framework and are instead encoded as distinct, event-specific representations. Our data suggest that memory traces for schema-incongruent events rely more heavily on vivid contextual details, and that inference in these cases depends on flexible retrieval mechanisms that reconstruct and recombine individual memory traces at the time of retrieval (see also, Kumaran & McClelland, 2012). Prior research has demonstrated that context reinstatement at retrieval can enhance associative inference (Cox et al., 2021; Liu et al., 2024). The current findings extend this by demonstrating that this effect is particularly relevant for schema-incongruent events.

Interestingly, retrieval-driven context reinstatement was associated with poorer memory for encoding context. This aligns with prior evidence of a trade-off between memory integration and retention of episodic details (Carpenter and Schacter, 2017, 2018). These results suggest that, for schema-incongruent events, reconstructive inference may come at the cost of contextual specificity.

We also observed schema deactivation during the encoding of schema-incongruent BC events. Exploratory analyses revealed that this deactivation was linked to the reinstatement of schemas congruent with the B word. This suggests that even when an event is globally incongruent with its context, the memory system may recruit a more congruent schema at encoding to facilitate the integration of overlapping information. Notably, this congruent-schema reinstatement was negatively associated with context reinstatement during AC test (**Figure 4B**), suggesting that when a congruent schema is recruited during encoding, inference may be supported by integration rather than by combining distinct memory traces at

retrieval. However, our schema and context memory test did not include the alternative schema that may have been reinstated for word B, preventing us from determining whether inference was structured around that specific representation. Future studies could address this limitation by systematically manipulating and testing the presence of multiple potentially relevant schemas. Such work could explore whether initially incongruent schemas are actively suppressed in order to form new, congruent representations that support the formation of integrative memory during encoding. This would offer deeper insight into the dynamic flexibility of schema engagement and its role in adaptive learning and memory.

Previous research has identified several boundary conditions that determine whether overlapping experiences are encoded as integrated or separated memory representations**,** including task demands (Richter et al., 2016), time (Zeithamova and Preston, 2017), encoding context (Cox et al., 2021; Liu et al., 2024), and individual differences (Bramão et al., 2025; Yu et al., 2025). The current findings add schema congruency to this list, highlighting it as a key factor that modulates the balance between integration and separation. Specifically, schema-congruent events are more likely to be integrated into unified memory representations, whereas schema-incongruent events tend to be maintained as distinct memory traces, relying on flexible retrieval for successful inference.

In summary, our findings underscore the dynamic nature of memory-based inference, demonstrating that the brain flexibly engages distinct encoding and retrieval mechanisms depending on the congruency between new experiences and prior knowledge. Schema-congruent events are primarily integrated during encoding, forming unified representations that span multiple experiences. This integrative process likely reflects the embedding of new information within existing schematic frameworks, supported by the medial prefrontal cortex (Gilboa and Marlatte, 2017; Bein and Niv, 2025). In contrast, schema-incongruent events are more often encoded as distinct memory traces, and the inference across them depends on the flexible retrieval and recombination of separated memory traces on demand, a process thought to be supported by a big-loop recurrence within the hippocampus (Koster et al., 2018). Together, these findings highlight how prior knowledge shape memory-based inferences and may guide further research on how other types of schemas, such as social and cultural generalized knowledge structures, influence inference and decision-making (Boeltzig et al., 2023)

## Data and Code Accessibility

Data and code will be made available on request.

## Author Contribution

ZL, MJ & IB – Conceptualization and Methodology; ZL – Investigation, Data Curation and Formal Analysis; ZL & IB – Visualization, Writing – Original Draft Preparation; ZL, MJ & IB – Writing – Review & Editing; IB & MJ – Supervision & Funding Acquisition.

## REFERENCES


Anderson JR (1981) Effects of prior knowledge on memory for new information. Mem Cognit 9:237–246.

Audrain S, McAndrews MP (2022) Schemas provide a scaffold for neocortical integration of new memories over time. Nat Commun 13:5795.

Bein O, Niv Y (2025) Schemas, reinforcement learning and the medial prefrontal cortex. Nat Rev Neurosci 26:141–157.

Boeltzig M, Johansson M, Bramão I (2023) Ingroup sources enhance associative inference. Commun Psychol 1:40.

Bramão I, Jiang J, Wagner AD, Johansson M (2022) Encoding contexts are incidentally reinstated during competitive retrieval and track the temporal dynamics of memory interference. Cereb Cortex 32:5020–5035.

Bramão I, Johansson M (2018) Neural Pattern Classification Tracks Transfer-Appropriate Processing in Episodic Memory. eneuro 5:ENEURO.0251-18.2018.

Bramão I, Liu Z, Johansson M (2025) Remembering the past affects new learning: The temporal dynamics of integrative encoding. Neuropsychologia 212:109148.

Brod G, Lindenberger U, Werkle-Bergner M, Shing YL (2015) Differences in the neural signature of remembering schema-congruent and schema-incongruent events. NeuroImage 117:358–366.

Carpenter AC, Schacter DL (2017) Flexible retrieval: When true inferences produce false memories. J Exp Psychol Learn Mem Cogn 43:335–349.

Carpenter AC, Schacter DL (2018) False memories, false preferences: Flexible retrieval mechanisms supporting successful inference bias novel decisions. J Exp Psychol Gen 147:988–1004.

Chelnokova O, Laeng B, Eikemo M, Riegels J, Løseth G, Maurud H, Willoch F, Leknes S (2014) Rewards of beauty: the opioid system mediates social motivation in humans. Mol Psychiatry 19:746–747.

Cox WR, Dobbelaar S, Meeter M, Kindt M, Van Ast VA (2021) Episodic memory enhancement versus impairment is determined by contextual similarity across events. Proc Natl Acad Sci 118:e2101509118.

Davies M (2008) Corpus of Contemporary American English. Corpus Contemp Am Engl Available at: https://www.english-corpora.org/coca/.

De Deyne S, Navarro DJ, Perfors A, Brysbaert M, Storms G (2019) The “Small World of Words” English word association norms for over 12,000 cue words. Behav Res Methods 51:987–1006.

Diana RA, Yonelinas AP, Ranganath C (2013) Parahippocampal cortex activation during context reinstatement predicts item recollection. J Exp Psychol Gen 142:1287–1297.

Eichenbaum H (1999) The hippocampus and mechanisms of declarative memory. Behav Brain Res 103:123–133.

Folkerts S, Rutishauser U, Howard MW (2018) Human Episodic Memory Retrieval Is Accompanied by a Neural Contiguity Effect. J Neurosci 38:4200–4211.

Frank D, Montaldi D, Wittmann B, Talmi D (2018) Beneficial and detrimental effects of schema incongruence on memory for contextual events. Learn Mem 25:352–360.

Ghosh VE, Gilboa A (2014) What is a memory schema? A historical perspective on current neuroscience literature. Neuropsychologia 53:104–114.

Gilboa A, Marlatte H (2017) Neurobiology of Schemas and Schema-Mediated Memory. Trends Cogn Sci 21:618–631.

Greve A, Cooper E, Kaula A, Anderson MC, Henson R (2017) Does prediction error drive one-shot declarative learning? J Mem Lang 94:149–165.

Han H (2020) Implementation of Bayesian multiple comparison correction in the second-level analysis of fMRI data: With pilot analyses of simulation and real fMRI datasets based on voxelwise inference. Cogn Neurosci 11:157–169.

Kass RE, Raftery AE (1995) Bayes factors. J Am Stat Assoc 90:773–795.

King J-R, Dehaene S (2014) Characterizing the dynamics of mental representations: the temporal generalization method. Trends Cogn Sci 18:203–210.

Koster R, Chadwick MJ, Chen Y, Berron D, Banino A, Düzel E, Hassabis D, Kumaran D (2018) Big-Loop Recurrence within the Hippocampal System Supports Integration of Information across Episodes. Neuron 99:1342-1354.e6.

Kumaran D, Hassabis D, McClelland JL (2016) What Learning Systems do Intelligent Agents Need? Complementary Learning Systems Theory Updated. Trends Cogn Sci 20:512–534.

Kumaran D, McClelland JL (2012) Generalization through the recurrent interaction of episodic memories: A model of the hippocampal system. Psychol Rev 119:573–616.

Liu Z, Johansson M, Johansson R, Bramão I (2024) The effects of episodic context on memory integration. Sci Rep 14:30159.

McClelland JL, McNaughton BL, O'Reilly RC (1995) Why There Are Complementary Learning Systems in the Hippocampus and Neocortex:InsightsFrom the Successesand Failuresof Connectionist Models of Learning and Memory. 102:419–457.

Miller JF, Neufang M, Solway A, Brandt A, Trippel M, Mader I, Hefft S, Merkow M, Polyn SM, Jacobs J, Kahana MJ, Schulze-Bonhage A (2013) Neural Activity in Human Hippocampal Formation Reveals the Spatial Context of Retrieved Memories. Science 342:1111–1114.

O'Reilly RC, Rudy JW (2000) Computational principles of learning in the neocortex and hippocampus. Hippocampus 10:389–397.

Ortiz-Tudela J, Turan G, Vilas M, Melloni L, Shing YL (2024) Schema-driven prediction effects on episodic memory across the lifespan. Philos Trans R Soc B Biol Sci 379:20230401.

Pham-Gia T, Turkkan N, Eng P (1993) Bayesian analysis of the difference of two proportions. Commun Stat - Theory Methods 22:1755–1771.

Richter FR, Chanales AJH, Kuhl BA (2016) Predicting the integration of overlapping memories by decoding mnemonic processing states during learning. NeuroImage 124:323–335.

Schlichting ML, Preston AR (2014) Memory reactivation during rest supports upcoming learning of related content. Proc Natl Acad Sci 111:15845–15850.

Schlichting ML, Preston AR (2015) Memory integration: neural mechanisms and implications for behavior. Curr Opin Behav Sci 1:1–8.

Shohamy D, Wagner AD (2008) Integrating memories in the human brain: hippocampal-midbrain encoding of overlapping events. Neuron 60:378–389.

Staresina BP, Gray JC, Davachi L (2009) Event Congruency Enhances Episodic Memory Encoding through Semantic Elaboration and Relational Binding. Cereb Cortex 19:1198–1207.

Tompary A, Zhou W, Davachi L (2020) Schematic memories develop quickly, but are not expressed unless necessary. Sci Rep 10:16968.

Treder MS (2020) MVPA-Light: A Classification and Regression Toolbox for Multi-Dimensional Data. Front Neurosci 14:289.

Tulving E, Kroll N (1995) Novelty assessment in the brain and long-term memory encoding. Psychon Bull Rev 2:387–390.

Van Kesteren MTR, Beul SF, Takashima A, Henson RN, Ruiter DJ, Fernández G (2013) Differential roles for medial prefrontal and medial temporal cortices in schema-dependent encoding: From congruent to incongruent. Neuropsychologia 51:2352–2359.

Van Kesteren MTR, Rignanese P, Gianferrara PG, Krabbendam L, Meeter M (2020) Congruency and reactivation aid memory integration through reinstatement of prior knowledge. Sci Rep 10:4776.

Van Kesteren MTR, Ruiter DJ, Fernández G, Henson RN (2012) How schema and novelty augment memory formation. Trends Neurosci 35:211–219.

Yu W, Duncan KD, Schlichting ML (2025) Using retrieval contingencies to understand memory integration and inference. Mem Cognit Available at: https://link.springer.com/10.3758/s13421-025-01727-8 [Accessed June 27, 2025].

Zeithamova D, Preston AR (2010) Flexible memories: differential roles for medial temporal lobe and prefrontal cortex in cross-episode binding. J Neurosci 30:14676–14684.

Zeithamova D, Preston AR (2017) Temporal proximity promotes integration of overlapping events. J Cogn Neurosci 29:1311–1323.

Zeithamova D, Schlichting ML, Preston AR (2012) The hippocampus and inferential reasoning: building memories to navigate future decisions. Front Hum Neurosci 6:1–14.