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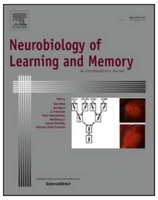

Brain activities of reconsolidation: Nuances in post-retrieval interference led to optimal alterations of episodic memories

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ABSTRACT

When memories are reactivated, they enter a period of instability in which they can be affected by a variety of follow-up manipulations. The existence of this type of memory reconsolidation offers the potential for clinical interventions of maladaptive memory. However, such potential cannot be fully exploited until the internal mechanisms of memory changes via reconsolidation are better understood. In the current study, we used a three-day AB-AC paradigm that included self-referential simulation processing and employed electroencephalogram (EEG) techniques to explore how post-retrieval updates of episodic memory come about. Behaviorally, we found that reactivation alongside interference learning (ReI-L, AB-AC, n = 52) can produce much more false memories compared to no reactivation new learning (New-L, AB-DC, n = 31) and reactivation repetitive learning (Rep-L, AB-AB. n = 30). More importantly, ERP results revealed that trials from ReI-L in which memory distortions subsequently occurred showed an observable (compared to the new-learning without memory reactivation) but attenuated (compared to trials associating with later intact memory) amplitude of frontal N400, indicating a moderate level of early conflict reactivation is necessary to trigger crucial memory instability. In addition, to promote optimal distortion of the original memory, a sufficient later constructional processing is also required, reflecting in these intrusive/later false trials showed a larger amplitude of late posterior negativity (LPN). A linear classifier employing neuro features of FN400 and LPN during the reconsolidation phase could predict the original memory retention with 72% accuracy. The present findings indicate that nuance in post-retrieval interference, moderate conflict with protracted construction can lead to optimal alterations of episodic memories.

1. Introduction

There is substantial evidence demonstrating that when memories are reactivated, they enter a period of instability during which they can be altered or updated by various interventions, thus undergoing a reconsolidation process (Lee, Nader, & Schiller, 2017; Nader & Einarsson, 2010; Nader & Hardt, 2009). The potential of memory “reactivation-interference-reconsolidation” as an intervention model that could be applied to mental disorders characterized by maladaptive memories has long been discussed (Ecker & Bridges, 2020; Elsey, Van Ast, & Kindt, 2018; Schwabe, Nader, & Pruessner, 2014). However, the functional mechanisms by which memory, especially episodic memory, can be reactivated-updated is not entirely clear. Neuroimaging studies have observed that reactivation-interference learning can specifically modulate the BOLD (blood oxygenation level dependent) signal of the left hippocampus (Forcato et al., 2016), induce a more efficient brain network compared with repetitive learning (Bavassi et al., 2019), and modulate the role of parietal and temporal lobes during memory updating (St Jacques, Olm, & Schacter, 2013). Unfortunately, these neural correlates of memory reconsolidation did not provide satisfactory answers for the boundary conditions *under which* memory instability and changes ultimately occur.

How a memory trace is reactivated or to what extent it is reactivated may substantially affect its destabilization. In the absence of empirical evidence in the field of reconsolidation, some researches focusing on initial consolidation proposes a particularly interesting hypothesis (non-

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monotonic plasticity hypothesis, NMPH). This hypothesis indicated a non-linear relationship between the strength of neural activation and its plasticity: when the activation is too weak, synapse/memory is unaffected; when the activation is too strong, synaptic connections strengthen, only moderate activation induces optimal synaptic weakening, thus inducing plasticity (Detre, Natarajan, Gershman, & Norman, 2013; Newman & Norman, 2010; Sinclair & Barense, 2019). However, this hypothesis has not yet been tested within the context of reconsolidation or in a multi-day memory paradigm. During memory reconsolidation, the intensity of memory re-activation is directly related to the expectation violation caused by the conflict between relived memory trace and the current novel information. Here, surprise or prediction error has long been thought to be the key to triggering memory instability (Exton-McGuinness, Lee, & Reichelt, 2015; Sevenster, Beckers, & Kindt, 2013, 2014; Sinclair & Barense, 2018). However, there is also a view holding that *too strong* conflict or expectation violation is not conducive to update the original memory; instead, it will be more inclined to facilitate forming independent traces (Li et al., 2017; Sinclair & Barense, 2019). Thus, a scheme to optimize memory instability may lie in moderate levels of reacivation and error induction. Nevertheless, this hypothesis awaits empirical support.

Furthermore, the way new information is learned after reactivation is equally critical to facilitate the directed reconsolidation. The intensity of new learning can affect the degree of memory updating, that greater erosion of the previous memories is related to stronger traces of interfering learning (van Schie, van Veen, Hendriks, van den Hout, & Engelhard, 2017). In addition, effective updating should be driven by a continuous accumulation of error resolution (Exton-McGuinness et al., 2015; Lee, Seo, & Jung, 2012). This error resolution involves constant interaction with the old and new information and may be represented as extended reconstructive processes when memory is episodic. Therefore, memory updating might be inseparable from sufficient resource input for post-retrieval learning.

It seems to be a promising proposal that moderate early conflict with strong post-reactivation learning can optimize the directed reconsolidation of episodic memory. In order to test this hypothesis, event-related potential (ERP) techniques can be employed to examine the specific period of memory reconsolidation. Given the high temporal resolution of ERP techniques, the different cognitive processes of a single event, i.e., the early reactivation phase and the post-retrieval interfering phase, can be well distinguished. Here, we focus on two components, frontal N400 and late posterior negativity (LPN), to represent the initial reactivation (conflict induction) and post-reactivation learning (conflict management) phase, respectively.

N400 is a classic ERP component representing early semantic violations (i.e., I am happy to eat a *sock*) and has long been extended to other nonlinguistic expectation violation situations (i.e., on the snowy mountain context, unexpectedly appeared a crab, see Kutas and Federmeier (2011) for review). In the field of memory, the N400 with relatively prefrontal distribution was related to the early novelty in traditional recognition tasks (Curran, 2000; Rugg & Curran, 2007), and in recent reviews, more associated with retrieval intention and some discrepancy processing (Leynes, Bruett, Krizan, & Veloso, 2017; Undorf, Amaefule, & Kamp, 2020). These implications of N400 make it an ideal representation of early reactivation and expectation violation intensity. In other words, N400 can be hidden when the processing of current information does not involve any reference to recent experience (i.e., low reactivation and low conflict); conversely, it will be conspicuous when memory is strongly recalled while encountering a conflict re-code (i.e., high reactivation and high conflict).

For the post-retrieval processing, we focused on the late posterior negativity (LPN) component; a negative-going ERP recorded at posterior sites with a latency occurring 1 s later. Rather than representing early conflict, this component is thought to relate to continuous error resolution (Coles, Scheffers, & Holroyd, 2001; Friedman & Johnson, 2000) and the episodic reconstruction processes of retrieval outcomes (Johansson & Mecklinger, 2003; Mecklinger, Rosburg, & Johansson, 2016). LPN can represent the consistent interaction between current information and old episodes and is modulated by the amount of information that is actually used to reconstruct prior episodes (Mecklinger et al., 2016). Therefore, it can be quite appropriate to characterize the learning process during reconsolidation, in which individual must manipulate the inner episodes involving both old and new information to integrate and resolve conflicts.

In the current study, we adapted an AB-AC design to produce a “retrieval-interference” manipulation of memory. On the initial day of learning, participants learned a series of picture scenes in which a particular contextual object, such as a box (i.e., A), represented the background to the core memory object, such as a spider (i.e., B). On the second day, item A was this time employed as a reminder to reactivate the original scene memory. However, on this occasion, this original background object was matched with a novel object, such as a teddy bear (i.e., a new core object, C), to form a new scene. Such manipulation is thought to influence the primary memory of the “A-B” combination and to update “B”. In order to be more consistent with a clinical application scenario, the emotional valence of B objects was set to be negative, and that of C objects was set to be non-negative. In addition, to increase the ecological nature of memory encoding, participants were requested to employ self-referential simulation as a learning technique. In other words, the participants had to imagine that they were in the scene, interacting with the objects in the picture. This promotes the overall effect of learning and makes the lab-controlled episodic memories relevant to the self.

Our research objectives were twofold. The first objective was to behaviorally verify that post-reactivation interference can produce an appreciable quantity of memory updates. To achieve this, we compared retrieval interference learning (ReI-L, AB-AC) with other two forms of control groups: 1) No reminder new learning in which participants learned completely new scenes on the second day without memory reminder (New-L, AB-DC), and 2) reactivation repetitive learning in which participants reactivated and repeated the first day learning without new information interfering (Rep-L, AB-AB). We suppose that reminder-interference learning (ReI-L) would lead to the most memory distortions compared to other groups.

The second and main objective of the current study was to investigate which neuro-processing patterns exert a substantial impact, through intrusions or alternations, on primary memory. To achieve this, we aimed to compare the neuroprocessing between reactivation-learning (ReI-L) and no reactivation learning (New-L) on Day 2. More importantly, we would further decompose the reactivation-learning condition into intrusive learning (ReI-Intrusive) and non-intrusive learning (ReI-Non-Intrusive) based on the outcomes for the memory test and conduct a comparison. This allowed us to examine what kind of neuro-interference process can ultimately lead to the updating effect.

As mentioned, we hypothesized that for memories to be updated, a medium level of early reactivation and conflict induction, indexed by median N400 response, might be required. Specifically, we predicted that the trials that finally influenced the original memory (ReI-Intrusive condition) would show a significant visible N400 compared to no reactivation learning (New-L), but a weakened N400 amplitude compared to the ReI-Non-Intrusive condition. In addition, we assumed that an adequate post-retrieval construction process index by larger LPN responses should be closely related to the successful memory updating. Thus, we predicted that ReI-Intrusive condition would show enhanced LPN amplitude relative to both New-L and ReI-Non-Intrusive condition. Further, if these assumptions were well tested, a classification model can be made using the neural characteristics (FN400 & LPN) produced on the reconsolidation day to predict outcomes of the original memory.

2. Methods

2.1. Participants

In the current experiment, 130 healthy university students (aged from 18 to 28) from Beijing, China volunteered to participate in the experiment. They were assigned into three groups according to the type of learning performed on the second day treating (ReI-L: reactivation-interference learning group, $n = 60$; Rep-L: repetitive learning group, $n = 35$; New-L: No-reactivation new learning group, $n = 35$). The sample size was pre-evaluated through power analysis using G*Power 3.1. Based on previous studies that refer to post-retrieval updating of episodic memory (e.g., Chan & LaPaglia, 2013), in which the mean effect size on reconsolidation associated amnesia/distortion was medium to large $f \sim 0.35$, calculations indicated that at least 84 participants for three-group design would be required to achieve 80% power. Here, the planned participants of ReI-L group were doubled. Because the neuro processing (ERP analysis) of ReI-L was the main concern of the current study. Trials within the ReI-L group would be further classified as sub-conditions of "ReI-Intrusive" and "ReI-Non-Intrusive" for comparison with each other and comparing with New-L group. In addition, according to previous ERP researches identifying a subsequent memory effect from the encoding phase generated general medium effect size, $d \sim 0.50$ (Friedman & Johnson, 2000), we assumed that the effect size of distinguishing memory consequences using ERPs from reconsolidation phase may be similar but smaller. Thus, a relatively conservative effect size evaluation of $d \sim 0.4$ was employed, requiring at least 52 participants to achieve 80% power for the condition comparison, i.e., "ReI-Intrusive" and "ReI-Non-Intrusive" (two tails). All participants checked and signed an informed consent form before the experiment and received a small payment as compensation (150 RMB). Finally, 113 participants who went through the whole procedure and provided complete data (ReI-L $n = 52$, Rep-L $n = 31$, New-L $n = 30$) were included in the final analysis. There were no significant differences in age ($F_{(2,110)} = 1.60, p = 0.207$), gender ratio ($\chi^2 = 0.86, p = 0.651$) or education level ($F_{(2,110)} = 1.35$, $p = 0.262$) among the groups. This study research was approved by the ethics committee of the Institute of Psychology at the Chinese Academy of Sciences and was carried out in accordance with the approved guidelines.

2.2. Main task

The completed task consisted of an experimental session across three days (Day 1: scenario learning; Day 2: ReI-L / Rep-L / (noRe) New-L; Day 3: testing) with about 48 h interval between each experimental session. The task diagram is shown in Fig. 1.

2.2.1. Day 1: Common scenario learning

All participants were required to view 44 scenes presented in monochrome. Each scene included two separate components: a) a background (BG), which provided context information of the event (e.g., a box of a specific shape) and b) a core object (CO), which illustrated the key content of the event (e.g., spiders). The two components (the BG plus the subsequent CO) constituted the scene with a specific meaning (information pertaining to the screening process and rating parameters, including discernibility, familiarity, BG-CO relevance, as well as the valence of these scenes are available in supplemental materials). We requested that participants attempt to view each scene in a self-referential manner. That is, participants were asked to imagine themselves interacting with the core objects in the scene. For each trial, the procedural sequence was as follows: first, a fixation point was presented for 1 s; then, the single BG was presented for 1 s; this was followed by the BG-CO combination scene, which was presented for 6 s. Participants were required to view each scene on two occasions, with a ten-minute break in between. Participants were then given a CO recognition test immediately, in which 44 old COs and an additional 30 new COs were included, and the old/new judgment within 6 s was required. The recognition correct rate of all participants ranged from 0.89 to 1, and there was no difference among the three groups, $F_{(2,110)} = 0.36$, $p = 0.702$). This demonstrated the homogeneity of the first-day learning levels among the three groups.

2.2.2. Day 2: Group manipulation and EEG recording

About 48 h (range from 45 to 51 h) after the initial learning day, participants were assigned to one of three groups which differed according to learning manipulations. We took a recording of EEG signals while participants performed the Day 2 task.

For the ReI-L (Reminder-interference Learning) group, by presenting the same BGs as those presented on Day 1, we aimed to reactivate the original memory of participants. Although BGs belonged to scenes viewed on Day 1, we matched them with new COs (also different from the COs in Day 1 recognition test), to form 44 new interfering scenes. The procedural sequence was as follows: fixation point was presented for 1–1.5 s randomly; this was followed by the interference scene (consist of original BG - new CO combination) which was presented simultaneously and lasted for 6 s. Participants were asked to view these scenes in a self-referential manner by visualizing these monochrome scenes and mentally forming a sentence involving the objects and the "I" pronoun. All the scenes were repeated three times in a block design, in which 44 scenarios were presented one by one firstly and then conducting another round of learnings with the sequence of scenes keeping random in each learning round.

For the Rep-L (Repetitive Learning) group, participants were presented with 44 original scenes (original BG - original CO combination) and asked to learn these scenes in the same way as the ReI-L group, that is, by visualizing these monochrome scenes and mentally forming a sentence involving the objects and the "I" pronoun. The procedural sequence was also the same with the ReI-L group. It should be noted that although the materials in the Rep-L group are the same as the first day, the learning methods are different. Rather than passively repeating exposure, the individual conducted a self-referential re-encoding of already experienced scenes.

For the (noRe) New-L (new learning) group, participants were presented with 44 completely new scenes (new BG - new CO combination). All COs in this group were the same as those provided to the ReI-L group. The learning requirements and procedural sequence were the same as those for the other two groups.

2.2.3. Day 3: Unexpected memory tests

After approximately 48 h (range from 45 to 51 h), all participants were given a memory test via an online testing platform (https://www.wjx.cn/) in the form of a cued recall task with the aim of examining their first day of learning. The participants did not know the specific content of the test before the testing day. During the testing, participants were presented with the BGs of the learning scene on the first day and were asked to report the COs that matched the BGs on the *first day* rather than the second day. Participants typed their responses without a time limit and were required to give a specific answer even if they were not fully confident about their answers. Reporting explicit forgetfulness was allowed but not be encouraged.

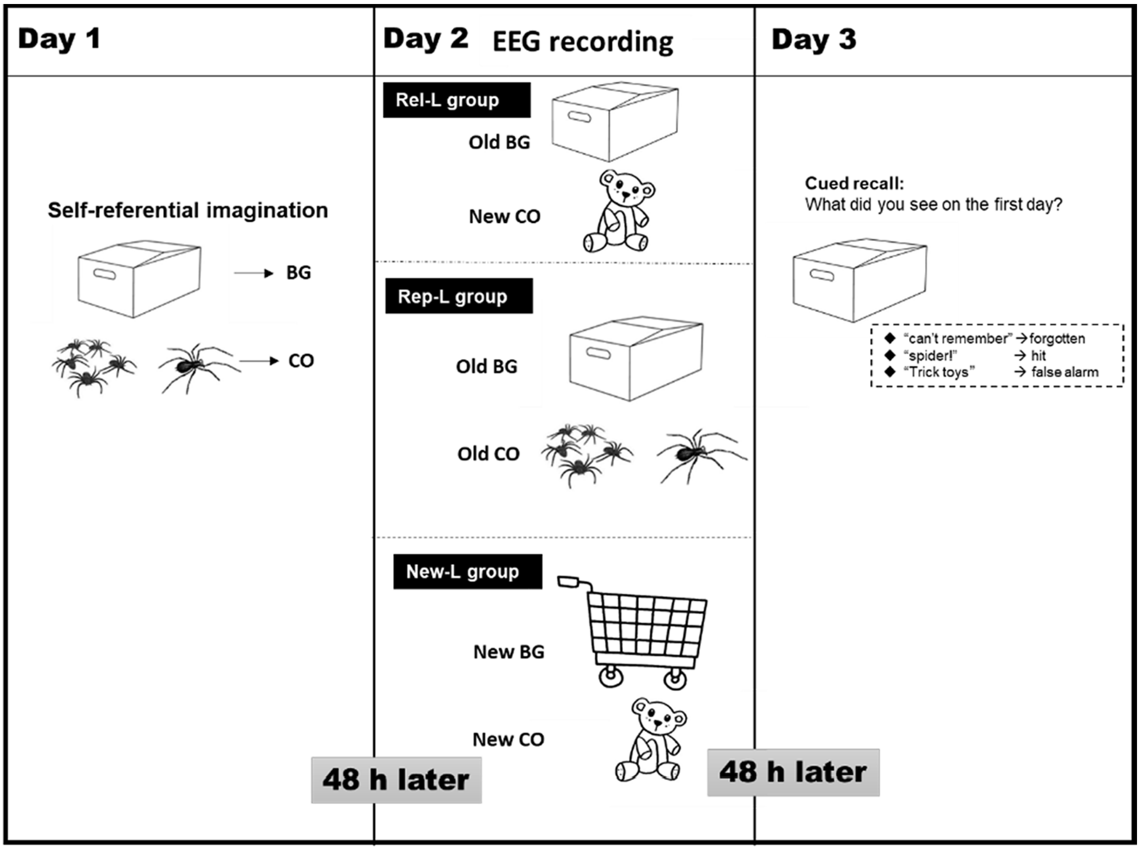

Fig. 1. General experiment procedure. The experiments consisted of three experimental sessions (learning, interfering, testing) with 48-hour intervals between each. On Day 1, all participants learned a series of negative scenarios (each one consists of the background, BG and the core object, CO) trial by trial through self-referential simulation, and rated the self-involvement level. On the Day 2, participants were divided into three groups randomly: a) Reactivation — Interference group, ReI-L, in which participants were reactivated the first-day memory via presenting the same background context with the Day 1, and interfered with the rematch scenarios with old backgrounds and novel objects; b) Reactivation — repetitive group, Rep-L, in which participants were reactivated and repeated the first-day memory via presenting the same background and objects with the Day 1; c) no Reactivation — new learning group, (noRe) New-L, in which participants were not reactivated the old memory deliberately, but were presented novel background and objects, even though these novel objects were the same as that in ReI-L group. Participants were required to learn these scenarios in a self-simulation manner, and EEG data were recorded on Day 2. On the testing day, all participants were conducted cued recall test for the first-day learning, in which the BGs of the first day were presented as the cue to require the participant's recall of its paired objects in Day 1. The participants' answers were divided into four categories: 1) correct recall, 2) false recall, 3) forgotten. The memory performance comparison among three groups, and ERP comparisons between ReI-L later correct trials and ReI-L later false recall trials with (noRe) New-L as the control were the main focuses of the current study.

2.3. EEG recording and processing

EEG was recorded during Day 2 (the group manipulation day) for all the participants from all three groups, but the group comparison was only conducted for the (noRe) New-L and ReI-L group given the confounding factors of inconsistent valence in the repetitive learning group[1]. Nevertheless, the further comparison of neuro-processing for conditions with distinguished memory outcomes within the ReI-L group was our primary focus.

For recording, a 64 Ag-AgCl electrodes cap (NeuroScan Inc., Herndon, VA, USA) was placed on the participants' scalp based on the extended International 10/20 system, with all electrode impedances maintained below 5 KΩ. EEG activity was amplified using a NeuroScan Synamp2 Amplifier with AC mode of 0.05–100 Hz band-pass filter and continuously sampled at a rate of 500 Hz. Offline EEG data were processed using EEGLAB (Delorme & Makeig, 2004). The signals were re-referenced to the averaged bilateral mastoids and filtered with a low-pass filter at 30 Hz (12 dB/oct). ERP data were segmented for each viewing trial using a time window of 5500 ms (500 ms pre-stimulus and 5000 ms post-stimulus) and baseline corrected using the pre-stimulus interval. Trials contaminated by eye blinks and movements were corrected using an Independent Component Analysis (ICA) algorithm (Jung, Makeig, Bell, & Sejnowski, 1998; D. Lee et al., 2012; Makeig, Bell, Jung, & Sejnowski, 1996). Trials under which voltage deviated more than 120 μV from baseline were rejected. Signals were averaged across trials and time-locked to the onset of the picture scene separately for conditions or labels.

In line with classical literature on electrode selection and time window setting of frontal N400 (Curran, 2000; Rugg & Curran, 2007) and LPN (Johansson & Mecklinger, 2003; Mecklinger et al., 2016), the N400 was represented by the mean amplitude of 250–550 ms time window from the grand average of prefrontal-central electrode sites (PF/AF/ F/ FC); while the LPN was characterized by the mean amplitude of 1000–4000 ms time window from the grand average of the posterior occipital electrodes (PO/O). The corresponding topographic maps of early (250–550) and late (1000–4000) ERP are presented to better

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[1] The EEG comparison between the three groups is not ideal here. In particular, the learning material of the repeated learning group was negative, while the material of the other two groups was perpetually neutral. ReI-L and New-L groups were comparable for the aspect of material valence. Note the comparison between the two groups can provide information about the differences in cognitive processes and the interpretation perspective of specific ERP responses.

illustrate the neural processing patterns under different conditions.

For the classification model, we extracted validated neural features that occurred during the reconsolidation phase and explore the possibility of memory outcome prediction via reconsolidation neuro-signatures. All artifact-free trials from ReI-L group participants were combined and normalized at the individual level. In order to reduce the dimensions of the features, the data were further down-sampled into 100 HZ, and the temporal-spatial characteristics of ERP were partially hypothesis-driven with the electrodes and time windows selection same as the ERP analysis (PF/AF/ F/FC/PO/O; 250–550 ms, 1000–4000 ms). Linear discriminant analysis (LDA) algorithm was executed for the single-trial data classification using the MatClassRSA toolbox (Wang, Norcia, & Kaneshiro, 2017) built-in MATLAB 2016a. MatClassRSA supports feature dimensionality using Principal Component Analysis (PCA), which is performed across the columns (features) of the 2D trials-by-feature EEG matrix X that is passed into the classifier, transforming the matrix to a trials-by-PC-feature matrix X_{PC}. Based on the number of PCs retained (K), only the first K columns of X_{PC} will be input to the classifier. Here in the current study, the number of principal components (PCs) was selected by setting the 'PCA' value of 0.9, which means selecting the most important features that explain 90% of the variance.

2.4. Data analysis

For the behavioral data, all answers collected from Day 3 (the testing day) were divided into three categories: 1) *correct recall*, reported the core object that correctly corresponded to the BG of Day 1; 2) *false recall*, reported the incorrect or distorted object that did not correspond to the BG of Day 1; 3) *forgotten*, explicit declaration of forgetting. The evaluation of recall answers was performed by two experimenters independently, ratings between experimenters were highly consistent (Cramer's $V_{(6072)} = 0.99$, $p < 0.001$). Any inconsistent judgments (<20) were reexamined and reclassified. Ratio parameters were calculated and indexed as correct rates, false rates and forgetting rates by dividing by the total number of trials. We conducted a one-way ANOVA and post-hoc analyses corrected by the Bonferroni method (or Tamhane method if the equal variances are not assumed) to reveal differences in memory performance among the three groups (ReI-L, Rep-L, New-L).

For the ERP data, the independent sample T-test between the ReI-L group and the (noRe) New-L group for two ERP indexes (N400 and LPN) was conducted firstly to clarify the processing significance of post-reactivation interfering compared with no reminder learning. More importantly, in order to explore neuro processing of post-retrieval interference that led to discriminative effects on primary memory within the ReI-L group, we divided all ReI trials into two main categories according to test outcomes from Day 3. First, "Intrusive" trials were made up of ReI trials that exerted a substantial effect on original memory by inducing false recall or memory distortion on Day 3 testing. Second, "Non-Intrusive" consisted of ReI trials that had no effect or maintained effect on memory; that is, the memory corresponding to Day 1's BG was intact and reported correctly on Day 3 testing. Here, even there is a forgotten category for the behavior classification, the number of "forgotten" trials was too small for ERP analysis (operationally, participants were encouraged to give a specific answer rather than reporting "forget"). Thus, forgotten trials were not included in the ERP analysis. Processing characteristics as reflected by FN400 and LPN amplitude according to these two types of trials (i.e., later false/ Intrusive vs later correct / Non-Intrusive) were compared via paired T-test.

For the single-trial ERP classification, outcome labels were set as 1 = correct (Non-Intrusive); 2 = false memory (Intrusive). LDA algorism with a ten-fold cross-validation method provided by MatClassRSA (Wang et al., 2017) was used to examine the accuracy of the prediction. In addition, the accuracy using a single ERP feature (i.e., 250–550 ms signals in frontal electrodes and 1000–4000 ms signals in posterior electrodes) were also evaluated and reported, respectively.

3. Results

3.1. Behavior memory performance

We observed significant differences in memory performance among the three manipulation groups (hit, $F_{(2,\ 108.8)} = 40.78$, $p < 0.001$; false recall, $F_{(2,88.0)} = 49.97$, $p < 0.001$; forgotten, $F_{(2,92,1)} = 5.95$, $p = 0.004$). The hit rate produced by the ReI-L group (M = 44.41%, SD = 27.65%) group was significantly lower than that produced by the Rep-L group (M = 88.12%, SD = 16.33%, $p < 0.001$) and the New-L group (M = 77.88%, SD = 20.17%, $p < 0.001$).

The false memory rate produced by the ReI-L group (M = 44.14%, SD = 24.98%) was significantly higher than that produced by the Rep-L group (M = 7.62%, SD = 8.73%, $p < 0.001$) and the (noRe) New-L group (M = 9.24%, SD = 13.58%, $p < 0.001$).

The forgotten rate of New-L group (M = 12.88%, SD = 12.06%) was significantly higher than that of the Rep-L group (M = 4.25%, SD = 10.02%, $p = 0.011$), and comparable with the ReI-L group (M = 11.45%, SD = 10.04%, $p = 0.931$).

Behavior results indicated that memory reactivation alongside interference learning could damage the original memory to produce more memory false. The memory performance for the three condition groups is illustrated in Fig. 2.

3.2. ERP results

3.2.1. N400

ReI-L group showed significantly larger early frontal negativity (N400) compared to the (noRe)New-L group, $t_{(80)} = 4.72$, $p < 0.001$, indicating reactivation interference learning has greater early reactivation intention or expectation conflict than no-reactivation new learning. In other words, the significant difference of N400 between two the groups indicates that N400 is reasonable to represent the early reactivation intention and expectation conflict since this processing does not exist in the No reactivation group.

Further paired t-tests revealed a significant difference within the ReI-L group for trials classed as *Intrusive* and *Non-Intrusive*. The Intrusive trials (i.e., later false trials) showed smaller negativity than Non-Intrusive trials (i.e., later correct trials), $t_{(51)} = 2.18$, $p = 0.034$, indicating that in order to make the original memory distorted, the post-retrieval interference process should include but should not have too strong early reactivation or too strong conflict processing, see Fig. 3a.

3.2.2. LPN

The New learning group and the general ReI-L group did not show significant difference on LPN index ($p > 0.05$), however, when ReI trials were decomposed, ReI-Intrusive trials showed the significant larger LPN

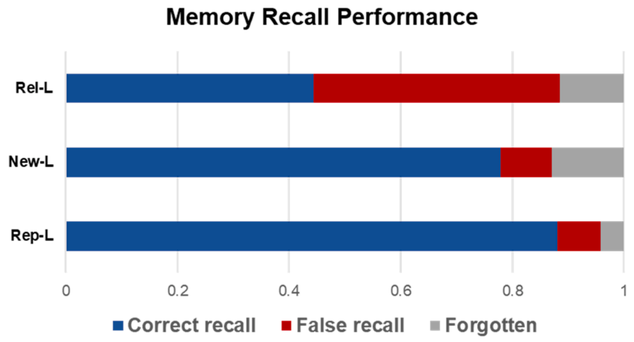
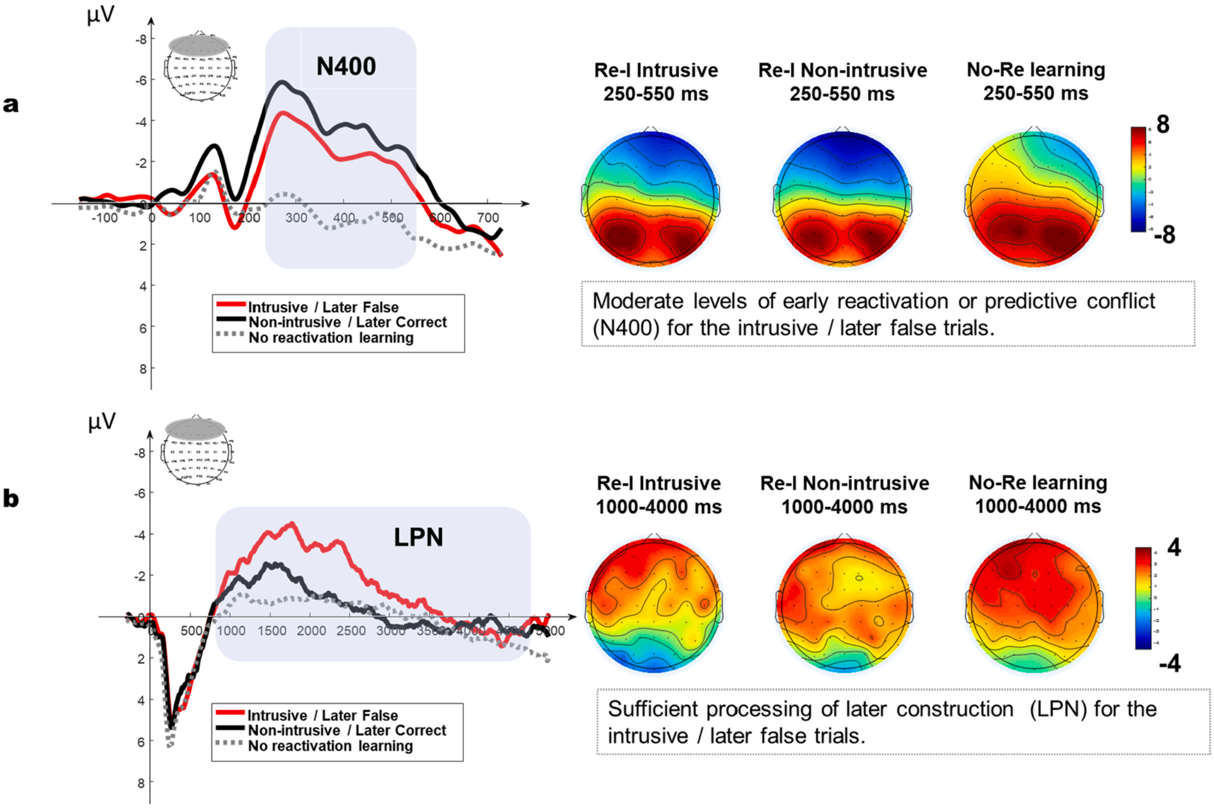


Fig. 2. Memory performance for each group. ReI-L, reactivation-interference learning group; New-L, no reactivation New learning group; Rep-L, repetitive learning group. The ReI-L group, in which original memories were reactivated and interfered with by new paired learning, showed the lowest correct recall rate and produced the most false memories for Day 1.



Moderate levels of early reactivation or predictive conflict (N400) for the intrusive / later false trials.

Sufficient processing of later construction (LPN) for the intrusive / later false trials.

Fig. 3. FN400 and LPN waveforms and topographic maps for the (No-re) New learning and Reactivation interfering learning condition with discriminative memory outcomes (Intrusive/later false & Non-intrusive /later correct). a) grand average waveform of prefrontal electrode sites (PF/AF/F/FC), the topographic map was represented by the time window of 250–550 ms, indicating the moderate early reactivation/conflict for Intrusive trials compared to the no reactivation learning and later correct trials (i.e., Non-intrusive); b) grand average waveform of posterior occipital electrodes (PO/O), the topographic map showed the later ERP (1000–4000 ms) distribution for different conditions, the later false (i.e., Intrusive) trials showed the more pronounced LPN (constructive processing) compared to new learning or later correct trials.

$t_{(70.7)} = 2.32$, $p = 0.023$ than no reactivation learning group, but it was not for ReI-Non-Intrusive trials $t_{(80)} = 0.86$, $p = 0.395$.

Besides, paired t-tests also revealed a significant LPN difference between Intrusive and Non-Intrusive trials, the Intrusive trials (i.e., later false trials) showed larger negativity than Non-Intrusive trials (i.e., later correct trials), $t_{(51)} = 2.36$, $p = 0.022$. These indicated a sufficient later construction process was required after moderate retrieval intention to interfere the original memory trace, see Fig. 3b.

3.2.3. Prediction model

We extracted the N400 (250–550) and LPN (1000–4000) responses in the prefrontal and posterior sites as classification features matrix, a total of 2816 artifact-free trials from all participants were fed into the classifier with the labels of later memory performance (later correct vs. later false). The LDA was performed and the 10-fold cross-validation calculated a prediction accuracy of 71.8%, which was significantly higher than the chance level (50%). Single features of early frontal components and later posterior components achieve 61.0% and 61.5%, respectively.

4. Discussions

Memory reconsolidation offers the potential for allowing clinical interventions to target maladaptive memories modifying (Phelps & Hofmann, 2019), and two essential components of processing involved in reconsolidation might lie in immediate reactivation of original memories and the subsequent interactive processing. In our episodic memory reconsolidation paradigm, we found that reactivation plus interfering learning can induce massive false memories compared to Rep-L and no reminder New-L control, indicating the phenomenon of post-retrieval updating. More importantly, our EEG results revealed that original memories are most likely unstable and influenced by subsequent interference learning when they are moderately reactivated and have a modest expectation violation. This is supported by the observation of medium amplitude of frontal N400 for those trials in which memory distortion subsequently occurred, compared to the new learning group and the later correct condition. Meanwhile, data also revealed that the reactivation interference condition, especially those trials that led to false memories, were associated with more significant LPN responses. This neural pattern indicates that in order to distort the original memory, a sufficiently long reconstruction or accumulated error resolution processing is required.

Although previous studies report that episodic memories can be disrupted or updated by new learning after reactivation (Chan & LaPaglia, 2013; Wirkner, Low, Hamm, & Weymar, 2015), this effect is not consistent, especially concerning memory that is autobiographical (Kredlow & Otto, 2015; Schwabe & Wolf, 2009, 2010). Our results are on the positive side that new learning after reactivation can disrupt the original memory, even if the memory is self-related. In fact, this self-involvement and agency of construction may facilitate the integration of interfering information into the original memory trace. The expansion of imagination and the diffusion activation of individual experience can be the frame of reference for memory distortion (Pan & Li, 2021).

However, the general inconsistency of results from reconsolidation researches suggests that the conditions that must be met to achieve memory updating are quite specific. Operationally, the first key process relates to how a memory is evoked and to what extent it is evoked. In previous studies, memory reactivation was usually achieved by presenting *a part* of the original representation. For example, in classical fear conditioning, half of the associative memory, typically the conditioned stimulus, would be presented in order to trigger the fear trace (Liu et al., 2014; Schiller et al., 2010). In declarative memory, a variety of reminders have been employed to reactivate memories. These have included the local cues of an entire episode (Forcato et al., 2016; Forcato et al., 2007; Forcato, Rodriguez, Pedreira, & Maldonado, 2010), the coding context (such as the basket containing the memory items) (Hupbach, Gomez, Hardt, & Nadel, 2007; Hupbach, Gomez, & Nadel, 2009; Hupbach, Hardt, Gomez, & Nadel, 2008), rapid serial visual presentation (Wirkner et al., 2015) and static fragments (Chan & LaPaglia, 2013; James et al., 2015) or editing clips (Sinclair & Barense, 2018) for dynamic video. Memory reactivation based on such methods is usually implicit and generally leads to incomplete memory expressions (Sinclair & Barense, 2019). Even reactivation was conducted via explicit recall instructions (Kredlow & Otto, 2015; Schwabe & Wolf, 2009, 2010; Suris, Smith, Powell, & North, 2013), retrospective processing can often be of a fuzzy and uncertain character.

In the current study, reminder-interfering trials that lead to memory distortions exhibited medium N400 amplitude comparing with no reminder control and the reminder trials that lead to correct recalls. Since N400 is a reliable indicator of retrieval intention and early conflict induction (Leynes et al., 2017), this electrophysiological data pattern can be an empirical demonstration of the moderate reactivation hypothesis. The rationale behind this “moderate reactivation optimization” is somewhat intuitive. If reactivation of the original trace is quite weak and no conflict was inducted, the memory trace is unlikely to be affected (Exton-McGuinness et al., 2015; Sinclair & Barense, 2018). However, if the recall of memory returns with excessive clarity, it stands to reason that the representation of the original memory could only be enhanced as the phenomenon of the “retrieval practice effect” (Karpicke & Roediger, 2008).

From the perspective of early exception violation, it can be assumed that the reactivation strength of the original memory directly determines the intensity of the initial prediction error. Behavior evidence showed that too large perceived differences of coding/recording contexts or learning/relearning contents could hinder the reconsolidation updating (Hupbach et al., 2007; Hupbach et al., 2008), suggesting excessive expectation violation might trigger an independent new memory trace, rather than a modification of the original one. Some evidence from fear conditioning showed that a CS reminder of moderate discrepancy (moderate partially reduplicated CS) could achieve the optimal effect of preventing fear relapse (Li et al., 2017), which also well fit the current idea in the context of episodic memory.

The non-monotonic plasticity hypothesis (NMPH) indicates that the function relating memory activation to learning is U-shaped. Strong excitation should result in memory strengthening and moderate excitation should result in memory weakening (Detre et al., 2013; Newman & Norman, 2010). Our data in the reconsolidation scenario extend this hypothesis with a new interpretation: weakened memory after mere moderate activation may be caused by some new learning or interference item that has not been explicitly observed. In any way, the individual does not inhabit an information vacuum after memory activation.

Apart from early reactivation and error induction, our data showed that sufficient post-retrieval interactive construction or the later error resolution processing could also be critical for final memory distortion. LPN could represent a process of constantly extracting information from the original experience in order to adapt to the current scene. This notion is quite consistent with the classical implication of this component as a constructive retrieval of the source memory (Johansson & Mecklinger, 2003; Mecklinger et al., 2016). We found that trials in which participants demonstrated distortions of memory exhibited distinctive larger and consistent LPN characteristics compared to the trials that were demonstrated correct recall. This may be because, for those memories that remained intact, the difference between the two days’ learning is apparent; thus, the impact of the post-retrieval interference can be rapid and limited. In this respect, later attention could be devoted solely to present learning, with no more continuous extraction activations required. However, for “subsequent false trials”, the associated larger negativity in the later period may have occurred as the result of a more elaborate level of processing consisting of deeper new learning alongside continuous extraction of original memories source.

However, the pattern of LPN in ReI-Intrusive trials may be inseparable from their previous median N400 presentation. In retrospect, it probably has been a moderate level of memory conflict (the forerunner condition) that offers the possibility of persistent interactive processing involving old and new information. Indeed, the pattern of neural changes immediately after retrieval, and the subsequent processing of new learning, must be interrelated: the former (retrieval) affects the latter (new learning) in a logic of time sequence, but the influence of the retrieval is revealed only when the new learning is initiated. Empirically, combinations of N400 and LPN responses during the reconsolidation phase in our data can predict the consequences of the original memory with an accuracy of significantly higher than the chance level, while no single factor can achieve the desired effect in the present sample. This suggests that the conditions that support successful memory updating are quite subtle. Perhaps, we may weaken the idea that there is a fixed moment with decisive condition when a memory loses its stability and instead, treat the whole retrieval and post-retrieval learning as a dynamic process of a continuum.

Of course, the prediction by neuro-indicators per se can be a straightforward illustration of the plasticity of memory and refer to the exciting logic behind the reconsolidation framework: the present determines the past. This operation also expands the psychological meaning of frontal N400 and LPN in a mainly encoding task but involving memory retrieval. They may be unique representations of the reconsolidation process and require more attention from future researchers.

Several limitations should be stated for the current study. In our study, the learning degree on day one was assumed to be consistent, but this may not be applicable to the single-trial level. If the neural activity of the initial coding can be collected and analyzed in combination with the neural changes in the reconsolidation stage, a more accurate prediction of final memory outcomes will be obtained. Nevertheless, the initial encoding of memory can hardly be intervened in real life, and it is still valuable of the current data to choose the reconsolidation interference phase as an observing window of memory dynamics. Secondly, the classification of memory recall can be relatively crude, especially in the ERP analysis, with the only category of “correct” and “false”, lacking further evaluation (e.g., the confidence level) of these reports. Specifically, we can see some heterogeneity in the false reports, like clear source errors and the fabrication of impressions with various confidence levels. It is possible that different post-retrieval interference processes may lead to different memory false or impairment patterns, which requires more accurate examinations that involve indicators for evaluating the nature of memory in various aspects. Third, even though our ultimate goal is to provide insights into maladaptive memory symptoms in mood disorders, our conclusions come from results produced by healthy participants. Individuals with dysthymia typically exhibit different memory characteristics (Dillon & Pizzagalli, 2018), so it is difficult to determine whether they follow the same process of memory retrieval updating as healthy individuals (Dunbar & Taylor, 2017; Fernandez, Pedreira, & Boccia, 2017). It is quite possible that these individuals might show specific abnormalities in reconsolidation-based memory updating, which could even be the root cause of their memory disruption (Beckers & Kindt, 2017). With this in mind, interventions that target specific potentially abnormal processes may be worth exploring. Another limitation of the study is that even negative images were used as memory material, and self-reference was employed to reinforce the involvement, this kind of artificial negative memory may still be qualitatively different from the real traumatic memories in clinical practice.

The current study paid more attention to updating episodic contents rather than their emotional significance, so updating the emotional burden of memory, or facilitating the emotion fading for negative events requires further attention. Relevantly, we noted that post-retrieval extinction might provide another paradigm to examine the updating of emotional components. While the current data cannot guarantee a consistent optimization principle for triggering destabilization and directing changes in different memory systems with fundamentally distinguished coding/storing mechanisms. However, considering reconsolidation as a cross-system memory phenomenon, we look forward to more systematic research and a potential integrated model for optimizing the updating and fading of traumatic memories.

In summary, the current study demonstrates that post-retrieval interference learning can induce significant distortions of episodic memory. ERP results characterize a basic neuro-processing that supports optimal memory changes. Moderate reactivation and error induction index by the medium amplitude of N400, with protracted reconstruction and conflict resolution indexed by significant amplitude of LPN, would facilitate episodic memory updating.

CRediT authorship contribution statement

Dong-ni Pan: Conceptualization, Methodology, Writing – original draft, Visualization. **Delhii Hoid:** Data curation, Investigation, Validation. **Oliver T. Wolf:** Writing – review & editing. **Xuebing Li:** Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.nlm.2021.107531.

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