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Post-encoding frontal theta activity predicts incidental memory in the reward context

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ABSTRACT

Memories for daily events require that individuals integrate initial fragile traces of events over time. Recent evidence suggests that reward anticipation enhances memory performance and amplifies frontal theta activity for remembered items vs. forgotten items. However, little is known about how incidental rewards after item presentation retrospectively modulate memory and the neural basis of this processing. Here, we used EEG combined with an incidental memory task to study how incidental reward association biased the post-encoding process. In the anticipatory stage, participants saw photos in win, loss and neutral contexts. Each photo was presented in a color frame that indicated the incentive condition (win vs. loss vs. neutral) and participants were asked to make a binary choice to predict whether the photo was associated with the left/right button. Feedback was presented to indicate arbitrary correctness and monetary outcomes. Recognition memory was tested after a short delay. During the encoding phase, left central-parietal theta power predicted subsequent memory performance in the win context. The post-encoding theta power at right central-frontal and central-parietal sites predicted later memory performance only in the win context. The size of frontal post-encoding related theta activity in the win context was correlated with the discriminate accuracy of the test stimulus. Our results suggest that post-encoding theta activity is closely linked to reward-based associative learning, providing evidence of a potential post-encoding mechanism of information binding.

1. Introduction

In daily life we encounter episodic events, some of which we later remember and some of which we forget. The subsequent memory effect (SME) refers to significant differences in the activation of particular brain regions during memory encoding of stimuli that are later remembered and stimuli that are later forgotten (Rugg, 1990). People are often motivated to remember some events better than others because of their importance, and in the context of psychological research, participants may anticipate rewards for better remembering. Indeed, previous studies have shown that the cognitive state before an event can influence the process of memory formation and retrieval (Guderian, Schott, Richardson-Klavehn, & Düzel, 2009; Rutishauser, Ross, Mamelak, & Schuman, 2010). These studies usually presented a cue preceding the onset of a stimulus and then analyzed the SME within this cue-stimulus interval (Gruber & Otten, 2010). E/MEG studies have demonstrated that the frontal theta (4–8 Hz) frequency band preceding the onset of a stimulus increased in response to the item that was subsequently recognized correctly (Addante, Watrous, Yonelinas, Ekstrom, & Ranganath, 2011; Fell & Axmacher, 2011). Further investigation of memory-related pre-encoding activation has focused on the effects of reward anticipation on SME. The pre-encoding encoding-related theta activity in reward anticipation can predict whether the stimulus will be remembered later, indicating that dopaminergic activity during reward anticipation impacts frontal theta activity (Gruber, Watrous, Ekstrom, Ranganath, & Otten, 2013). Increased frontal theta activity during a delay period has been shown to be positively correlated with visual working memory capacity (Kawasaki & Yamaguchi, 2012), suggesting that frontal theta activity is associated with enhanced motivation and attention. Together, the cognitive resources and motivational factors before an event may be associated with an active preparation for the event.

Many fMRI studies have shown that increased brain activation in the medial temporal lobe (MTL) and inferior prefrontal cortex is associated with memory formation (Strange, Otten, Josephs, Rugg, & Dolan, 2002). Brain oscillations in the memory domain have also been

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investigated extensively. Human and animal studies have shown that during the encoding stage, SME was associated with brain oscillations indexed by theta oscillation (4–8 Hz) (Summerfield & Mangels, 2005), beta oscillation (12–20 Hz) (Hanslmayr, Spitzer, & Bäuml, 2008), and gamma frequency band (55–70 Hz) (Osipova et al., 2006). The results of these studies suggest that brain oscillation activity during stimulus encoding plays a significant role in predicting subsequent memory performance.

However, the brain activity associated with consolidation that occurs immediately post-encoding has been less explored. Research on memory consolidation would suggest that initial memory for events could potentially be promoted if post-encoding meaningful information is tied to prior encoded events. Neuroimaging studies have indicated that post-encoding brain activities can predict working memory as well as long-term memory (Bergmann, Rijpkema, Fernández, & Kessels, 2012). A modified subsequent memory paradigm, with a fixation period (4–16 s) immediately after a movie clip was presented, has been used to investigate how offline processing immediately following an event offset encodes the episodes into memory. The results showed that bilateral hippocampus and caudate activations time-locked to stimulus offset predicted subsequent memory (Ben-Yakov & Dudai, 2011). These offline brain activities may reflect the episodic binding of information over the time course of the episodes and registration to memory of integrated episodes. Another possibility is that the post-encoding activity is associated with the initial stages of memory consolidation. A recent study, using a different approach in which a post-encoding cue instructed participants to remember or to forget the preceding stimulus, indicated that post-encoding ventral posterior parietal cortex (vPPC) activity was positively correlated with subsequent memory and was involved in the consolidation of cortically binding features of the prior stimulus (Elman, Rosner, Cohn-Sheehy, Cerreta, & Shimamura, 2013). These studies suggest a significant role of immediate post-encoding brain activity in predicting memory performance.

Rewards may selectively and retroactively promote memory performance. Past studies found the dopaminergic memory consolidation effect during reward anticipation, indicating increased motivation and attention in the intentional memory paradigm (Mather & Schoeke, 2011; Shohamy & Adcock, 2010). For example, participants have better recognition memory performance for task-related stimuli when there is a monetary incentive signaling a reward cue prior to the target stimuli. According to the post-encoding mechanisms of consolidation effects, rodent research has shown that post-encoding presentation of salient events such as reward or novelty predict subsequent memory of a previously encoded stimulus (de Carvalho Myskiw, Benetti, & Izquierdo, 2013). One study found that reward-motivated effects on retroactive memory enhancement generalized to conceptually related items on a 24-h memory test but not on an immediate recognition test (Patil, Murty, Dunsmoor, Phelps, & Davachi, 2017), suggesting the significant role of consolidation in reward-mediated memory enhancements. These studies showed that rewards motivated retroactive memory, and such enhanced performance might be explained in terms of increased motivation and attention in the stage of memory consolidation. Other studies also found the memory enhancement effect using incidental learning paradigms in which the test stimuli are used as targets in the reward learning task ; for example, participants were told that the speed with which they responded to the target pictures would determine gain or loss outcome, and then they performed a surprise recognition memory task. A recent study documented retroactive memory enhancements when the neutral stimulus was immediately followed by an unrelated reward cue in the absence of motivation (Murayama & Kitagami, 2014).The extant research provides evidence of the retroactive memory enhancement effect of reward-based learning on prior encoded items. This raises the question of whether and how task-irrelevant reward following a test stimulus retroactively influences memory formation at both the behavioral and neural level. Our study used an incidental memory paradigm to examine how extrinsic rewards immediately following the test stimulus influence memory formation.

Punishment also motivates goal-driven behavior in learning and memory. Previous fMRI studies in animals and humans have indicated that substantia nigra/ventral tegmental areas (SN/VTA) have stronger activation in response to cues associated with both upcoming reward and punishment (i.e., aversive electric shock) during memory encoding (Bauch, Rausch, & Bunzeck, 2014; Lammel et al., 2012). Studies using EEG and MEG techniques have shown that nociceptive events modulate neural oscillatory activity (Mancini, Longo, Canzoneri, Vallar, & Haggard, 2013). Furthermore, during incidental memory encoding, anticipation of aversive electric shocks modulates low beta power (14–30 Hz) (Bauch & Bunzeck, 2015), which suggests a neural mechanism by which aversive motivational factors can improve memory formation. However, there has been little systematic comparison between the neural bases of reward- and punishment-driven memory enhancement.

To understand the relationship between motivated context, post-encoding processes and memory formation, we conducted an EEG study using an incidental memory paradigm to investigate whether a post-encoding reward context without increased anticipatory motivation can retroactively predict subsequent memory of a previously encoded stimulus. Because rewards are incidental and not contingent on performance, we expect the behavioral effect of incidental rewards to be weak or not significant. However, neural responses might be more sensitive to our manipulation. We propose that the theta frequency band during stimulus encoding produces a positive subsequent memory effect (positive SME). Furthermore, we test the correlation between brain activity and behavioral memory activity as a way to identify potential brain mechanisms by which reward-related information without motivation may modulate the post-encoding theta activity immediately following the stimulus.

2. Method

2.1. Participants

Twenty-three healthy right-handed volunteers were recruited to take part in the EEG study. Three participants who had more than 75% of trials rejected were excluded from further analysis. Therefore, twenty participants' EEG data were included in the analyses (10 females; age mean ± SD, 20.40 ± 1.62 years old). All subjects had normal or corrected-to-normal vision, and no neurological or psychiatric disorders. All subjects provided written informed consent according to protocols approved by the South China Normal University Institutional Review Board.

2.2. Experiment procedure

2.2.1. Stimuli

We used 360 images of faces selected from the Chicago Face Database (http://faculty.chicagobooth.edu/bernd.wittenbrink). We counterbalanced by gender (male, female) of the face stimuli and randomized the presentation of faces appearing in the win, loss and neutral contexts across participants. Participants performed an encoding task and an incidental test task (see Fig. 1 for schematic illustration of trial design). There were 180 face stimuli used in the encoding phase, with 60 faces for each context (win, loss and neutral), and 180 face stimuli used in the test phase.

2.2.2. Encoding phase

With respect to the encoding task (see Fig. 1 A), a fixation cross was firstly shown with a jittered inter trial interval (ITI) varying between 1.75 s and 2.25 s (mean 2 s). Afterwards, a neutral face stimulus was presented on the screen. Participants were told that each photo was pre-assigned to be associated with the left or right button, and they had to

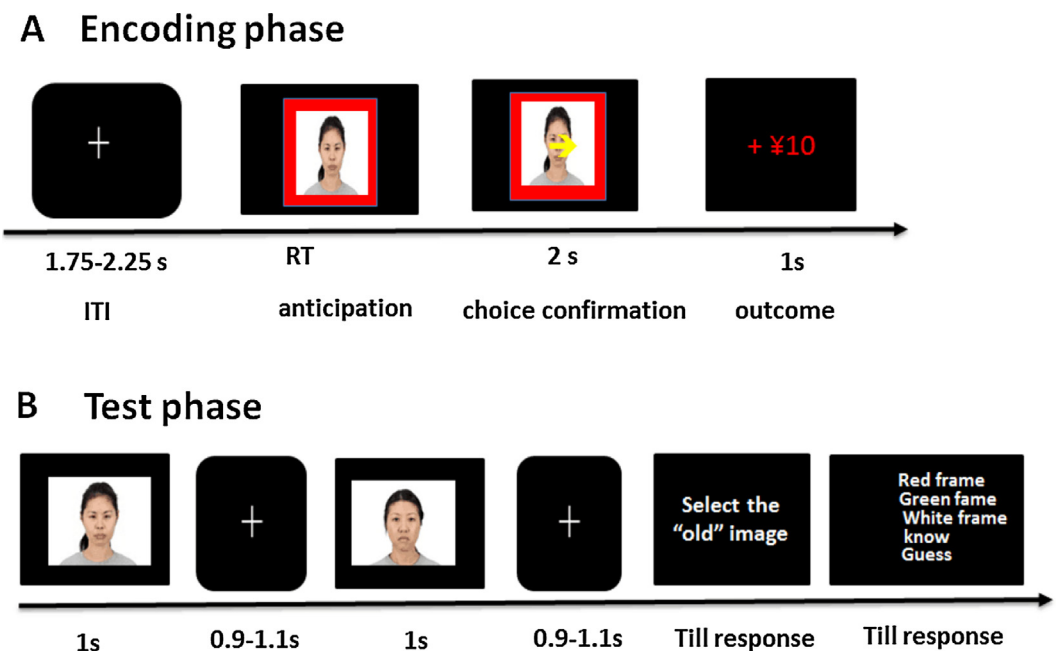

Fig. 1. Experimental Procedure. (A) Encoding phase. A neutral face stimulus was presented followed by a fixation. Participants were told that each photo was pre-assigned to be associated with the left or right button, and they had to make a choice (left or right) to predict whether the photo was predetermined to be associated with the left or right. If their prediction matched the arbitrary association, they performed correctly. Otherwise, their choice was wrong. There were three incentive contexts: win, loss and neutral. A correct choice led to winnings of ¥10 in the win context and no loss in the loss context, whereas a wrong choice led to no winnings in the win context and a loss of ¥10 in the loss context. Thus there were six different possible outcomes: win correct, win error, loss correct, loss error, neutral correct and neutral error. (B) Test phase. There was a 5-minute rest period. Then participants completed a surprise memory task. On each trial, with one face (for 1 s) being preceded by the other face (for 1 s), participants had to indicate which face they had seen by pressing the appropriate "1" or "2" button at their own pace. After participants made their choices, they performed a meta-memory task in which they were asked to indicate which incentive context the stimulus was in during the encoding phase (until response). They did this by responding to five options, in particular, the "red frame" meant win context, "green frame" meant loss context, "white frame" meant neutral context, "know" meant the participant was confident about the selection but did not retrieve details about the context, and "guess" meant there was no feeling of familiarity with or confidence in the selected option. There were 180 trials in the test phase.

make a choice (left or right) to predict whether the photo was predetermined to be associated with the left or right. If their prediction matched the arbitrary association, they performed correctly. Otherwise, their choice was wrong. There were three incentive contexts: win, loss and neutral, and each context was signaled by three different colored frames: red frame meant win context, green frame meant loss context and white frame meant neutral context. A correct choice led to winning ¥10 in the win context and no loss in the loss context, whereas an erroneous choice led to no winnings in the win context and a loss of ¥10 in the loss context.

Once participants made a choice, confirmation was provided by the presentation (for 2 s) of a yellow arrow, pointing from the face stimulus to the participant's choice (left or right). Then one of six possible outcomes was presented on screen (for 1 s): red ¥10 represented a gain of ¥10 in the win condition (*win correct*), red +¥0 represented a gain of ¥0 in the win condition (*win error*), green −¥0 represented a loss of ¥0 in the loss condition (*loss correct*), green −¥10 represented a loss of ¥10 in the loss condition (*loss error*), white +¥0 represented a gain of ¥0 in the neutral condition (*neutral correct*), and white −¥0 represented a loss of ¥0 in the neutral context (*neutral error*).

There were 180 trials, with 60 trials in each of the three anticipation contexts. In each context, the correct answer was on the left side in 30 trials and on the right side in 30 trials, with sequences being pseudorandomly assigned. The actual performance (correct or incorrect) was determined by participants' responses, resulting in a nearly equal number of trials in each condition. Participants were told that they would receive an extra reward, punishment or ¥0 by randomly choosing the outcome of one game after finishing the experiment. All participants received around ¥50 as compensation for taking part in this experiment.

2.3. Test phase (incidental memory)

Fifteen minutes later, participants completed a surprise memory recognition task (see Fig. 1 B), in which we probed item memory (i.e., recognition memory for face stimuli) and source-memory (i.e., the encoding contexts for the "old" stimuli). In each trial, participants were shown two face stimuli, with the presentation of one face (for 1 s) being followed by another face (for 1 s). One face was previously shown during the encoding task (i.e., "old") while the alternative face was never shown (i.e., "new"). Participants had to indicate which face they had seen by pressing the appropriate "1" or "2" button at their own space. The jittered inter-trial interval (ITI) between these two faces varied between 0.9 s and 1.1 s (mean 1 s). After participants made a judgment for the "old" item, they performed a source-memory test asking which incentive context the stimulus was in during the encoding phase (until response): red frame meant win, green frame meant loss, white frame meant neutral, "know" meant confidence in the selection despite not retrieving details about the context, and "guess" meant there was no feeling of familiarity with or confidence in the selected option. There were 180 trials in the test phase.

2.4. EEG recording and analyses

Brain electrical activity was recorded at 64 scalp sites using tin electrodes mounted in an elastic cap (NeuroScan 4.5) according to the International 10–20 system, with the reference to the left mastoid. The vertical electro-oculogram (VEOG) was recorded from left supra-orbital and infra-orbital electrodes. The horizontal electro-oculogram (HEOG) was recorded from electrodes placed 1.5 cm lateral to the left and right external canthi. All electrode impedances were maintained at less than 5 kΩ. The EEG and EOG were recorded from SynAmps DC amplifiers

and were continuously sampled at 1000 Hz/channel for off-line analysis. The experiment was conducted in an electrical laboratory with dim illumination and noise attenuation, administered on a Lenovo computer in CRT display with 1024*768 resolution, and controlled by E-prime2.0 software for presentation and timing of stimuli.

EEG data were preprocessed using EEGLAB toolbox (Delorme & Makeig, 2004) in MATLAB. The EEG data were resampled to 250 Hz and re-referenced off-line to linked mastoid electrodes using the average of the left and right mastoids. An additional 50 Hz notch filter was enabled to suppress line noise.. After rejecting manually any muscle artifacts and bad channels, the continuous EEG data were subjected to Independent Component Analysis (ICA). To remove ocular artifacts, independent components that were sensitive to eye-movement artifacts were identified and removed. The EEG data were high-pass filtered with a cutoff value of fc = 0.05 Hz, using the default FIR filter implemented in EEGLAB: a least-squares linear-phase filter of order 16500 with a transition bandwidth (the range of frequencies between the bandcut and the bandpass) of 0.05 Hz was run forward and backward. All trials in which EEG voltages exceeded a threshold of ± 70 μV during the recording epoch were excluded from analysis (Sun & Yu, 2014).

Because the pre-encoding period was a jitter fixation (from 1.75 s to 2.25 s), EEG was epoched from 1.7 s before the stimulus to 2 s after the stimulus onset. In the post-encoding period EEG was epoched from 1.5 s before outcome onset to 2.5 s after outcome onset. These relatively long epochs allowed us to investigate ERSPs from a low (3 Hz) to a relatively high (45 Hz) frequency. EEG baseline-subtracted in the time domain from −200 to 0 ms was used for artifact rejection and correction (Addante et al., 2011). We computed ERSP from 3 to 45 Hz using a modified complex sinusoidal wavelet with a 1116-ms wide sliding window and a wavelet factor of .78 (leading to an increase from 3 cycles at 3 Hz to 9.9 cycles at 45 Hz). For the pre-encoding and encoding stages, we removed half of the sliding window (645 ms) at the edges (i.e., the beginning and the end) of each epoch, leaving an epoch between −1438 and 1142 ms after edge removal. For the post-encoding stage, to reduce the potential edge effects, we removed half of the sliding window (720 ms) at the edges (i.e., the beginning and the end) of each epoch, leaving an epoch between −942 and 1938 ms after edge removal. For the pre-encoding and encoding stage, a baseline in the frequency domain was not employed; although it is commonly used for this procedure, we mainly focused on the differences in oscillatory power between trial types (Fell & Axmacher, 2011; Guderian et al., 2009). For the post-encoding stage, a time window between −500 to −200 ms before outcome onset was used as a baseline for ERSPs. The mean number of trials in each condition (remembered and forgotten trials in each incentive context) was higher than 30 trials.

2.5. Statistical analyses

According to previous studies assessing encoding related theta activity (Addante et al., 2011; Gruber et al., 2013), an across-trial permutation test was used to test for significant differences in pre-encoding, encoding and post-encoding related theta activity, separately. The 1.7 s interval of the pre-encoding stage was collapsed into 17 time windows of 100 ms each; the 2 s interval of encoding (anticipation stage) was collapsed into twenty time windows of 100 ms each; the 1 s interval of post-encoding (outcome stage) was collapsed into ten time windows of 100 ms each. For each time window, mean power between 4 and 6 Hz, where theta activity was most evident, was calculated for each electrode in each trial for each participant. The permutation tests were performed in each time window to reveal electrode clusters with significant pre-encoding, encoding and post-encoding related theta activity.

Two-tailed t tests were firstly calculated at each electrode site. Then the trials were randomized and split in half into two pseudo conditions, and t tests were used to compare the pseudo conditions. This procedure was repeated 1000 times. The obtained pseudo t values were sorted in ascending order, yielding a distribution of 1000 values. Finally, the two tails from the pseudo t value distribution were used as the critical t values to reject the null hypothesis. Using an alpha level of 0.05 and 1000 permutations, the 25th and 975th values represent the critical t values. This procedure was conducted for all 64 scalp electrodes and would therefore be expected to lead to a Type 1 error on 3.2 electrodes (64*0.05) per time window assuming independence across sites. We only considered effects that spanned across four electrodes and interpreted significant clusters that spanned across two consecutive time bins. If the significant effects spanned two consecutive time bins, another permutation test was run in this extended time window.

3. Results

3.1. Behavioral results

We conducted a 3 × 2 analysis of variance (ANOVA) in which incentive (win vs. loss vs. neutral) and performance (correct vs. error) were within-subjects variables, and hit rate (calculated as successful recognized memory accuracy) was the dependent variable. The main effects of incentive and performance were not significant, $F(2,38) = 1.62$, $P = 0.21$, $\eta_p^2 = 0.078$ and $F(1,19) = 1.84$, $P = 0.19$, $\eta_p^2 = 0.088$, respectively. The interaction effect was not significant ($F(2,38) < 1$, $P = 0.79$, $\eta_p^2 = 0.012$) .

3.2. ERSP results

3.2.1. Pre-encoding related theta activity

We found that theta power between −900 ms and −700 ms before stimulus onset was significantly higher for remembered trials than for forgotten trials on a cluster of right central-parietal sites (see Fig. 2). No such effect was found in the win and neutral conditions. Further analysis showed that theta power difference in remembered versus forgotten trials in the loss context was significantly larger than that in the win and neutral contexts (see Fig. 3).

3.2.2. Encoding related theta activity

We found that the encoding related theta activity, as evidenced by differences in theta power between later remembered and forgotten trials, was significant in the win context but not in the loss or neutral context. Specifically, significant differences were found between 700 and 1300 ms after the stimulus onset on a cluster of left central-parietal electrode sites (see Fig. 4). In the win context, theta power difference in the 700–1300 ms interval predicted whether the stimuli were remembered or forgotten in the following memory recognition test. However, there was no significant interaction between encoding related theta activity (SME) across win, loss and neutral contexts.

3.2.3. Post-encoding related theta activity

Our main interest was how unrelated win and loss information modulates post-encoding theta oscillation activity and memory formation. The difference in EEG power at theta frequency band 4–6 Hz between later remembered and forgotten trials (i.e., the subsequent memory effect) in the win context was enhanced around 500–700 ms following the outcome onset at right central-frontal and central-parietal electrode sites (see Fig. 5 A). However, permutation tests on the difference in theta power between remembered and forgotten trials were not significant in the loss and neutral contexts (see Fig. 5 B, C). Further analyses found that the interaction of the subsequent memory effect (SME) between the win, loss and neutral contexts was significant. A difference in post-encoding related theta activity (i.e., later remembered minus later forgotten trials) was found between the win and neutral context, where a significantly increased theta power between 500 and 700 ms was found in the win context compared to the neutral context (see Fig. 6).

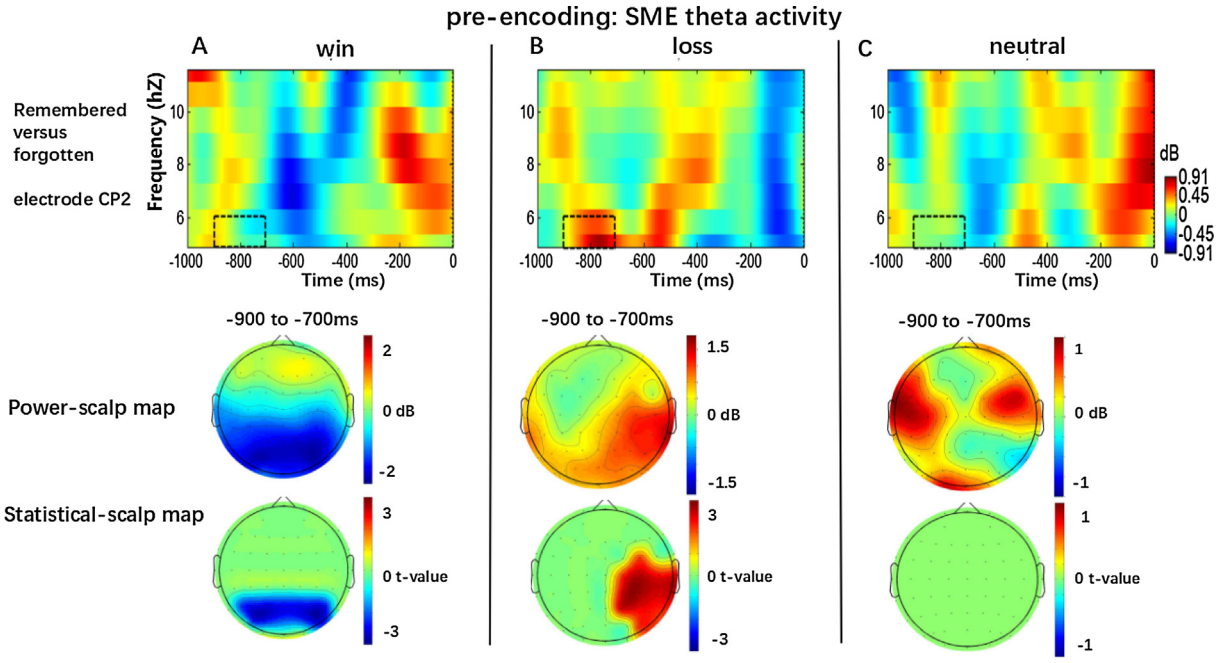

Fig. 2. Pre-encoding related theta activity in win, loss and neutral context. Win context (A), loss context (B), neutral context (C). Top row: time frequency representations of difference between the stimuli that were later remembered and later forgotten (i.e., encoding-related activity) in theta oscillatory power (4–6 Hz) at CP2 site. Middle row: Scalp maps depicting the location of pre-encoding encoding-related theta activity in the −900 to −700 ms interval before the stimulus onset. Bottom row: statistical scalp maps corresponding to the power scalp maps displayed in the middle row. The maps show the statistics of the permutation tests on theta power (4–6 Hz) in the −900 and −700 ms interval before the stimulus onset. The color coding represents the value of the *t* statistics where significant differences were found ($p < 0.05$). The pre-encoding encoding-related subsequent memory effects in the theta oscillation power were found at the right central-parietal sites only in the loss context.

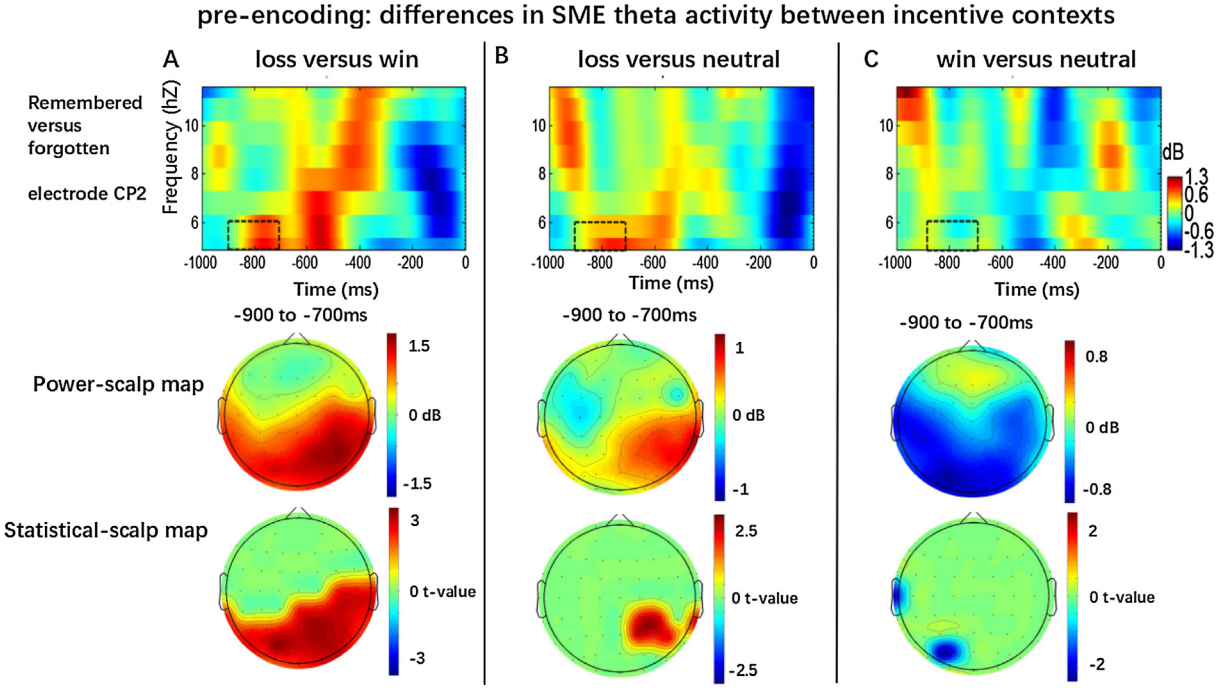

Fig. 3. The difference in pre-encoding related theta activity (remembered versus forgotten) among win, loss and neutral contexts. (A) loss versus win contexts, (B) loss versus neutral contexts, (C) win versus neutral contexts. Top row: time frequency representations of difference in pre-encoding related theta activity (later remembered trials versus later forgotten trials) at CP2 between win, loss and neutral contexts. Middle row: Scalp maps depicting the location of difference in pre-encoding related theta activity between the −900 and −700 ms before the stimulus onset. Bottom row: statistical scalp maps corresponding to the power scalp maps displayed in the middle row. The maps show the statistics of the permutation tests on pre-encoding encoding-related theta power in the −900 and −700 ms interval before the stimulus onset. The color coding represents the value of the t statistics where significant differences were found ($p < 0.05$). A significant difference in pre-encoding encoding related theta activity was found between the loss versus neutral, and loss versus win contexts.

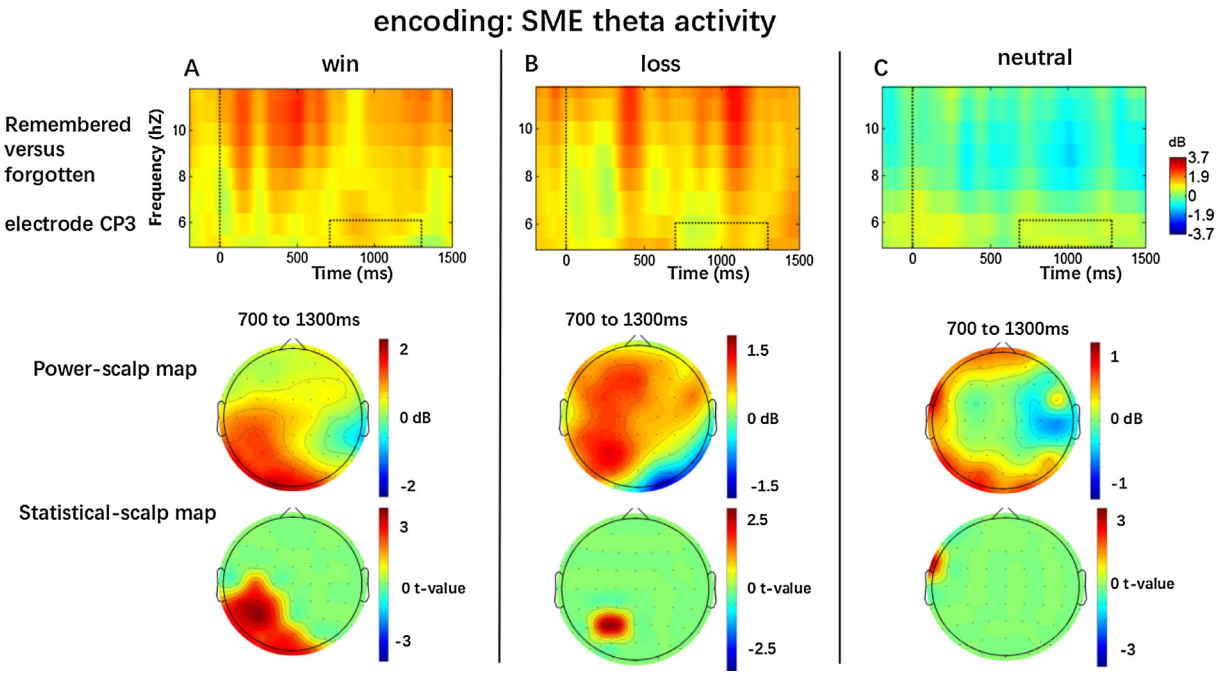

Fig. 4. Encoding related theta oscillation power for subsequent memory performance. (A) win context, (B) loss context, (C), neutral context. Top row: time frequency representations of the difference between stimuli that were later remembered and later forgotten (i.e., encoding-related activity) in theta oscillatory power (4–6 Hz) at CP3 site. Middle row: Scalp maps depicting the location of encoding-related theta activity in the 700–1300 ms interval at the encoding phase. Bottom row: statistical scalp maps corresponding to the power scalp maps displayed in the middle row. The maps show the statistics of the permutation tests on encoding-related theta power in the 700–1300 ms interval. The color coding represents the value of the *t* statistics where significant differences were found ($p < 0.05$). The encoding-related subsequent memory effects in the theta oscillation power were found at the left central-parietal sites only in the win context.

To further understand the role of post-encoding theta power in the reward-related context for memory formation, we calculated an across-subject correlation between the size of post-encoding related theta activity (i.e., remembered versus forgotten trials) and participants' overall recognition memory accuracy in the win context. We conducted the analysis separately for the electrode sites showing significant subsequent memory effects in the win context. All twenty participants were included in the analysis. We found that the difference in theta power

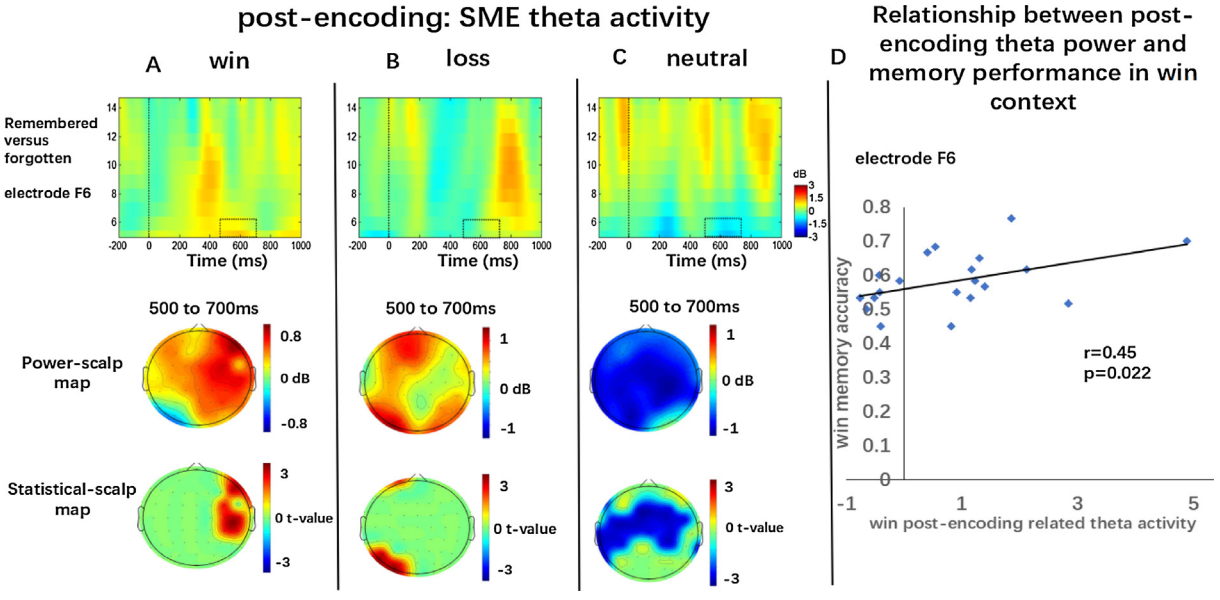

Fig. 5. Post-encoding related activity in theta power for subsequent memory effects. (A) win context, (B) loss context, (C) neutral context. Top row: time frequency representations of theta oscillation power for incentive contexts and subsequent memory performance (later remembered and forgotten) at F6, separated by trials. Middle row: Scalp maps depicting the location of post-encoding related theta activity (i.e., later remembered trials versus later forgotten trials) in the 500–700 ms interval at the outcome stage. Bottom row: statistical scalp maps corresponding to the power scalp maps displayed in the middle row. The maps show the statistics of the permutation tests on encoding-related theta power in the 500–700 ms interval. The color coding represents the value of the *t* statistics where significant differences were found ($p < 0.05$). The post-encoding related subsequent memory effects in the theta oscillation power were found at the right central-frontal and central-parietal sites in the win context. (D) A scatter plot showing the relationship between the post-encoding subsequent memory effect in theta power and memory accuracy in the win context is presented for electrode F6.

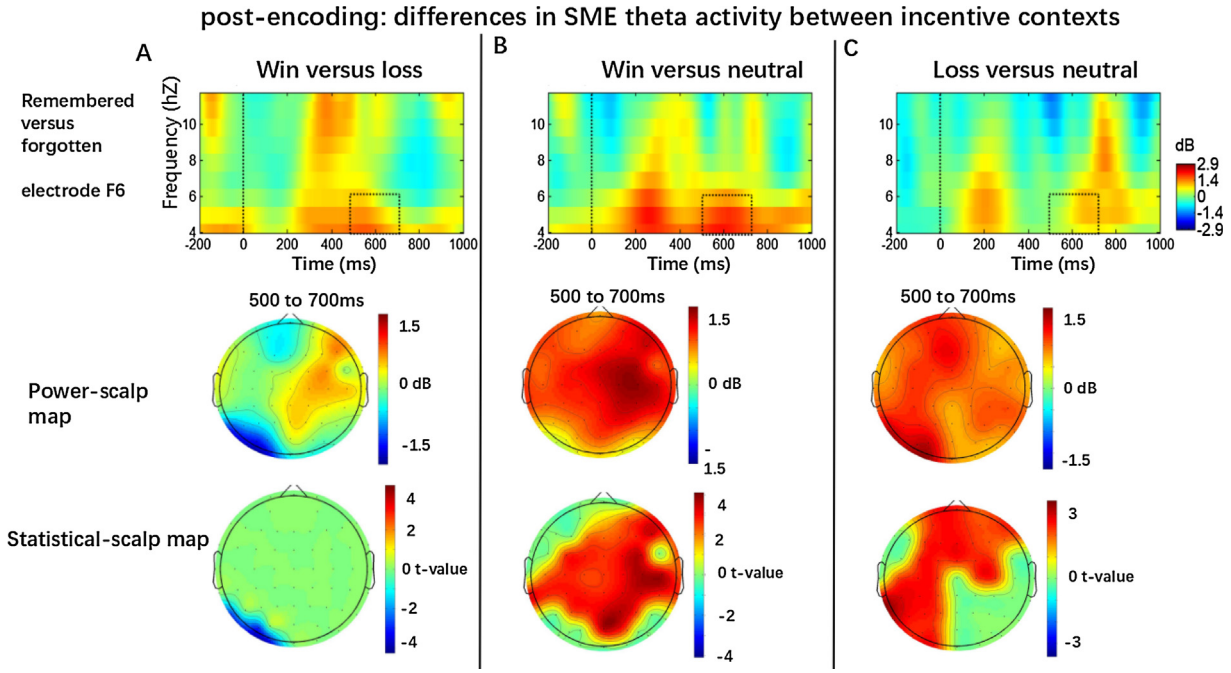

Fig. 6. The difference in post-encoding related theta activity (remembered versus forgotten) between win, loss and neutral contexts. (A) win versus loss contexts, (B) win versus neutral contexts, (C) loss versus neutral contexts. Top row: time frequency representations of difference in post-encoding related activity (later remembered trials versus later forgotten trials) at F6 between win, loss and neutral context. Middle row: scalp maps depicting the location of difference in post-encoding related theta activity in the 500–700 ms interval between win, loss and neutral contexts. Bottom row: statistical scalp maps corresponding to the power scalp maps displayed in the middle row. The maps show the statistics of the permutation tests on encoding-related theta power in the 500–700 ms interval in the outcome phase. The color coding represents the value of the t statistics where significant differences were found ($p < 0.05$). A significant difference of post-encoding related theta activity was found in the win versus neutral context.

between later correctly recognized and later forgotten stimuli in the win context in the 500–700 ms immediately following the test stimuli was correlated with participants' recognition accuracy . The correlation was specific to a cluster of frontal electrode sites (FC4: $r = 0.40$, $p = 0.041$; F6: $r = 0.45$, $p = 0.022$) that showed significant post-encoding related theta activity (positive subsequent memory effect) in the win context. A scatter plot showing the relationship between the post-encoding subsequent memory effect in theta power and memory accuracy in the win context is presented for electrode F6 (see Fig. 5 D).

We also focused on the post-encoding related effects of incentive (win vs. loss vs. neutral) and performance (correct vs. error). Firstly, we found that the difference between the error and correct trials was significant only in the win context. The results showed that the increased theta power in the 500–700 ms interval on a cluster of frontal sites depended on whether the task was performed incorrectly or correctly (see Fig. 7). There was no significant difference between the error and correct trials in the loss and neutral context. Furthermore, we found that on a cluster of frontal sites the difference in theta activity between the error and correct trials was significantly increased in the win context compared to the loss and neutral contexts (see Fig. 8).

According to the source memory performance, we further examined the effect of confidence judgment on the memory formation. Because trials in which participants reported being certain of their correct source memory (judged the correct frame's colour for the "old" stimulus and could retrieve details about it) were scarce (averaged less than 5 trials), we combined the trials for "correct with certainty" source memory and the "know" trials as the "high confidence" trials. The "guess" trials and the incorrect source memory trials (judged the incorrect frame's color for "old" stimulus) were combined as the "low confidence" condition. Based on the confidence judgment, a permutation test was used to test for the significance of differences in theta power for the subsequent memory effect (high confidence trials versus forgotten trials) in the pre-encoding, encoding and post-encoding stages. Permutation tests on the theta activity difference between the remembered and forgotten trials did not reveal the incentive context effect in these three stages, as evidenced by the lack of significant SME effects in either the win, loss or neutral context.

4. Discussion

The purpose of our study was to explore whether neural oscillation activity immediately post-encoding is related to subsequent memory. Consistent with our hypotheses, post-encoding related frontal theta activity was modulated by irrelevant reward information. The pre-encoding theta power at right central-parietal sites between −900 and −700 ms before test stimulus onset was related to successful memory formation in the loss context. However, in the anticipation stage, the left central-parietal theta power in 700–1300 ms predicted the subsequent memory performance (i.e., stronger theta activity for the remembered stimuli than for the forgotten stimuli) only in the win context. At the post-encoding stage, power in the theta bands was found to be significantly increased in the error condition compared to the correct condition only in the win context. Importantly, theta power at the central-frontal and central-parietal sites immediately post-encoding predicted later memory performance only in the win context, with increased oscillatory activity in the theta band for remembered stimuli than for forgotten stimuli. Moreover, the difference in frontal theta power between remembered versus forgotten trials was positively correlated with memory accuracy in the win context. These findings suggest that post-encoding related theta activity in the reward context can retroactively predict memory performance, which may reflect episodic binding of previously encoded stimuli. Our study also has implications for understanding the underlying mechanism of encoding and post-encoding processes.

Our study firstly indicated that the pre-encoding theta activity between −900 and −700 ms before the stimulus onset was related to

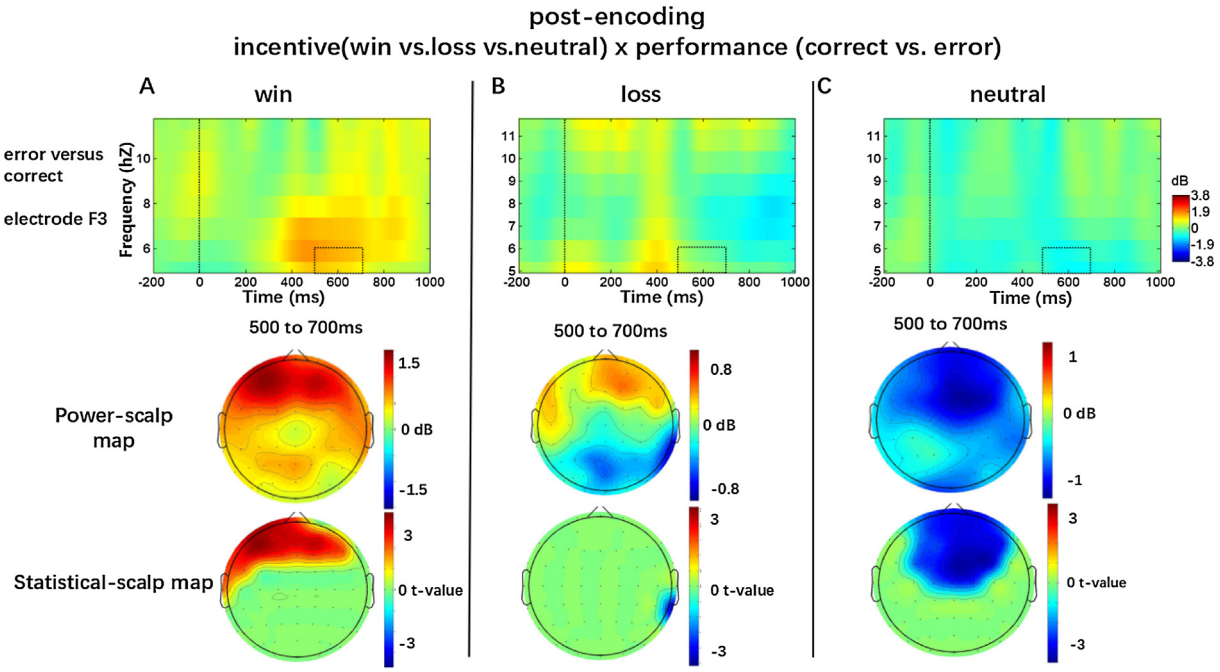

Fig. 7. Theta oscillation power for incentive context (win, loss and neutral) and outcome evaluation (correct and error). (A) win context, (B) loss context, (C) neutral context. Top row: time frequency representations of theta oscillation power at F3 for incentive contexts and outcome evaluation, separated by trials. Middle row: scalp maps depicting the location of theta activity difference between error and correct trials in each incentive context in the 500–700 ms interval. Bottom row: statistical scalp maps corresponding to the power scalp maps displayed in the middle row. The maps show the statistics of the permutation tests on theta power (4–6 Hz) in the 500–700 ms interval at the outcome phase. The color coding represents the value of the *t* statistics where significant differences were found ($p < 0.05$). The theta oscillation power difference between the error and correct trials was found at the frontal sites only in the win context.

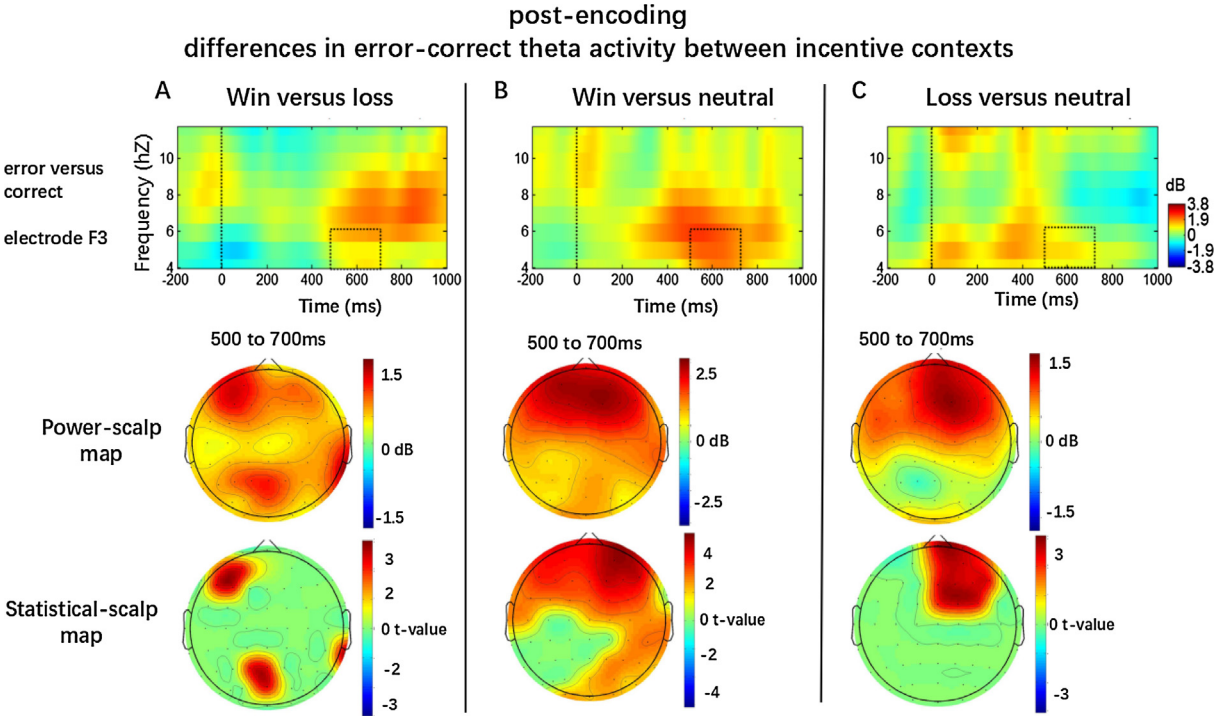

Fig. 8. The difference in error versus correct among win, loss and neutral contexts. (A) win versus loss contexts, (B) win versus neutral contexts, (C), loss versus neutral contexts. Top row: time frequency representations of difference between error and correct trials in theta oscillation power (4–6 Hz) at F3. Middle row: scalp maps depicting the location of theta activity in the 500–700 ms interval in the outcome phase. Bottom row: statistical scalp maps corresponding to the power scalp maps displayed in the middle row. The maps show the statistics of the permutation tests on theta power in the 500–700 ms interval in the outcome phase. The color coding represents the value of the t statistics where significant differences were found ($p < 0.05$). Differences in the outcome evaluation (error versus correct trials) were found at the frontal sites in win versus loss and win versus neutral contexts.

memory formation in the loss context. Research has indicated that pre-encoding theta activity can predict later successful memory information (Guderian et al., 2009; Salari & Rose, 2016),and theta activity may be crucial as an influence on the stimulus encoding process in hippocampus and in interactions between this encoding and other brain activity (Düzel, Penny, & Burgess, 2010; Rutishauser et al., 2010). We also demonstrated the link between theta activity during stimulus encoding and successful memory formation. We found an increased encoding related theta power (higher theta power for remembered items than for forgotten items) at left central-parietal sites during stimulus encoding phase in the win context. Numerous EEG studies have reported increased frontal theta activity during memory encoding for stimuli that are later successfully remembered than forgotten (Hanslmayr et al., 2008; White et al., 2013). Our study further indicated the relationship between theta activity in reward and punishment contexts pre-encoding and in the encoding stage.

Importantly, we found that theta power at right central-frontal and central-parietal sites immediately following the test stimulus (post-encoding related theta activity) can predict subsequent memory only in the win context. It has been shown that monetary reward can enhance memory encoding and storage, for example, one study showed that pre-encoding theta oscillation activity was associated with successful memory performance during the anticipation of high reward but not low reward (Gruber et al., 2013), which suggests that frontal theta activity influences memory encoding via anticipatory reward-related consolidation processes (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006). Alternatively, this memory enhancement effect may reflect a link between encoding-related theta activity and stimulus-context binding via enhancement of reward-related motivational cues (Tort, Komorowski, Manns, Kopell, & Eichenbaum, 2009). Our study provides further evidence of this reward enhancement effect on post-encoding processes by documenting stronger theta power for the remembered compared to forgotten stimulus. Together, these results document the modulatory effect of reward information in post-encoding related brain neural oscillation activity.

The results of previous studies suggested that encoding processes create the initial memory representation and post-encoding processes impact the memory process via consolidation (Hamann, 2001). Research has found that the consolidation effects of the post-encoding process can be generated for prior presented neutral (Judde & Rickard, 2010) and positive stimuli (Liu, Graham, & Zorawski, 2008). This post-encoding process can be modulated by emotional arousal (Wang & Sun, 2017), stress (compared to a no-stress condition) (Yonelinas, Parks, Koen, Jorgenson, & Mendoza, 2011) and reward learning (Patil et al., 2017). Studies with rodents have suggested that in the period within seconds following encoding, hippocampal cells rapidly replay sequences of activation that occurred during encoding, in forward or reverse order (Diba & Buzsáki, 2007). Reverse replay sequences mainly take place in post-encoding rest periods within seconds and are suggested to reflect binding between event sequences and the outcome (Carr, Jadhav, & Frank, 2011). Similarly, research with humans also found that hippocampus and caudate activations during the immediate (4–16 s) post-encoding period were correlated with subsequent memory performance (Ben-Yakov & Dudai, 2011), which may require binding of information and integration of episodes as cohesive internal units in memory. In line with these studies, we suggest a possible mechanism by which stimulus-context binding of irrelevant reward information immediately following a stimulus plays a crucial role in successful memory formation.

Retroactive and proactive mediated memory enhancement may occur by means of two separate mechanisms. Previous studies have shown that the anticipation of rewards can improve memory when recognition performance in a later test is tied to reward. In these studies, a reward cue was firstly presented, and participants would receive extra monetary rewards if they correctly recognized the encoded stimuli in the later test phase. These studies indicated that extrinsic rewards promote memory consolidation by activating the mesolimbic reward system and can be explained in terms of increased motivation and attention. However, salient events such as those associated with rewards and novel events following encoded neutral stimuli can retroactively improve memory, a phenomenon called the “retroactive memory enhancement effect”. Rodent research has demonstrated that salient events post-encoding can promote memory for previously presented stimuli (Salvetti, Morris, & Wang, 2014). Studies with humans have found that rewards (Patil et al., 2017), emotional learning (Dunsmoor, Murty, Davachi, & Phelps, 2015) and conceptually related information produce retroactive memory enhancement. According to a neurobiological account of memory consolidation (Redondo & Morris, 2011), there is a synaptic tagging and capture (STC) mechanism by which encoded stimuli activate a synaptic “tag”, and salient events following the stimuli increase protein-synthesis mediated consolidation of prior events. Furthermore, a recent study found that rewards without increased motivation create a retrograde enhancement of memory for prior irrelevant neutral events presented in close temporal proximity to reward cues (Murayama & Kitagami, 2014). Our study extends these findings by exploring the neural representations of retroactive memory enhancement effects in incidental reward learning. In contrast to the win context, the memory predictive effect of immediate (within seconds) post-encoding processes disappeared in the loss context. In feedback monitoring, previous research found that reward probability modulated theta power following a win but not following a loss (Cohen, Elger, & Ranganath, 2007). It is possible that theta activity of the SME is specific to the win context, but the underlying mechanism of this effect could be explored further. Furthermore, previous studies on retroactive memory found that significant memory enhancement effects appeared in the 24 hours delayed recognition test but not in the immediate memory test (Murayama & Kitagami, 2014; Patil et al., 2017). In our immediate recognition study, it is possible that incidental one shot reward learning may have weak effects on recognition test due to the lack of sufficient memory consolidation. Future studies may explore whether incidental rewards impact memory 24 hours after encoding.

Additionally, with regard to the post-encoding processes, the frontal theta power was larger in the error than in the correct condition in the win context, whereas there were no significant differences between the error and correct conditions in the loss and neutral contexts. We further examined the differences in error-related theta activity (i.e., differences in theta power between error and correct trials) between the win, loss and neutral contexts. Significant differences were found between 500 ms and 700 ms after the outcome onset. Specifically, the difference in theta power between error and correct trials was significant in the win context but not in the loss or neutral context on a cluster of right frontal electrode sites. Previous studies have indicated that increased theta activity was related to erroneous responses (Gevins, Smith, McEvoy, & Yu, 1997; Luu, Tucker, & Makeig, 2004). Similarly, the feedback-related theta power for losses was larger than that for gains (Cohen et al., 2007). These findings suggest that higher theta oscillation activity is associated with negative outcomes. Consistent with previous patterns, we also found higher theta oscillation activity for incorrect versus correct responses in the win context.

In conclusion, our study indicated that post-encoding theta oscillation activity predicted subsequent memory performance only in the context of winning, suggesting that reward based associative learning immediately following a test stimulus can benefit memory formation. We suggest a possible mechanism by which irrelevant post-encoding reward information may retroactively improve the integration and binding of the prior encoded stimulus over time, thus successfully predicting later memory performance. Using an incidental memory paradigm, we further demonstrated the neural representatives of the effects of post-encoding reward information on memory formation even without increased motivation. These findings advance our understanding of the neural basis of encoding and post-encoding processes, which may contribute to further investigation of human memory

formation.

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