Neuropsychologia 50 (2012) 2839–2848

Contents lists available at SciVerse ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Suppression of aversive memories associates with changes in early and late stages of neurocognitive processing

Chunping Chen [a,b], Chao Liu [a,*], Ruiwang Huang [a,c], Dazhi Cheng [a], Haiyan Wu [a], Pengfei Xu [a], Xiaoqin Mai [d], Yue-Jia Luo [a,*]

[a] State Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, Beijing, 100875, China
[b] Key Laboratory of Mental Health, Institute of Psychology, Chinese Academy of Sciences, Beijing, 100101, China
[c] Center for Studies of Psychological Application, Guangdong Key Laboratory of Mental Health and Cognitive Science, South China Normal University, Guangzhou, 510631, China
[d] Department of Psychology, Renming University, Beijing, 100872, China

ARTICLE INFO

Article history:
Received 22 September 2011
Received in revised form
28 June 2012
Accepted 4 August 2012
Available online 15 August 2012

Keywords:
Memory suppression
Event-related-potentials
Later negativity (LN)
Late parietal positivity (LPP)
Think and No-Think task

ABSTRACT

Unwanted memories, such as emotionally negative, can be intentionally suppressed through voluntary control in humans. Memory suppression is thought to be mediated by the interplay of a chain of neurocognitive processes. However, empirical data in support of this notion is lacking. Using high-temporal resolution event-related potential (ERP) technique, we investigated the time course of ERPs associated with suppression of negative and neutral memories in a Think/No-Think paradigm in young, healthy participants. Results showed that participants had greater difficulty in suppressing emotionally negative memories than neutral ones. ERPs and source analyses demonstrated that memory suppression processing for negative and neutral memories were generally associated with changes during early components of a time window of 70–260 ms, such as P1 and N2, mainly at the right inferior frontal gyrus and occipital lobe; suppression of aversive memories was associated with two major late ERP components between 380 and 800 ms, with significantly smaller later negativity (LN) but larger late parietal positivity (LPP), primarily at the right medial and superior frontal gyri. These results suggest that differences in early components may reflect early stages of suppression processing including visual awareness, attention reallocation, and executive processing. Differences in late components between suppression of aversive and neutral memories may reflect a process of down-regulating conscious recollection of memory representations supported by prefrontal and parietal networks. A less effective control of this process, as evidenced by smaller LN and larger LPP, may explain the fact that emotionally negative memories were harder to be suppressed. Altogether, these findings suggest that suppression of aversive memories requires down-regulation of late conscious recollection, which can be dissociated from early visual and attention processing in memory suppression.

1. Introduction

Behavioral and neuroscience studies have shown that previously learned materials can be successfully suppressed by voluntary control (Anderson & Green, 2001; Anderson et al., 2004; Banich et al., 2009; Depue, Banich, & Curran, 2006; Depue, Curran, & Banich, 2007; Hauswald, Schulz, Iordanov, & Kissler, 2011; Minnema & Knowlton, 2008). Voluntary forgetting can be achieved through stopping memory retrieval, which is supported by intentional inhibitory mechanism (Anderson, 2005; Anderson & Levy, 2009; Levy & Anderson, 2002). One of the most used paradigms to examine such a voluntary memory suppression effect is the Think/No-Think (T/NT) task. In this task, participants are first presented with pairs of two unrelated items. Then, the participants are presented with the first item of the pair (cue) and asked to recall (Think condition) the second item (target) or asked to consciously not recall the second item (No-Think condition). Finally, the participants are asked to recall all items. Typically, the repetitive presentations of No-Think trials lead to the impaired subsequent recall of target information compared to the baseline items that are presented initially but do not appear during the T/NT phase (Levy & Anderson, 2002). This impaired recollection is called negative control effect (Anderson & Levy, 2009), whereas memory performance for the No-Think items are impaired relative to the Think items, known as total control effect (Anderson & Levy, 2009).

Using the T/NT task, Anderson and Green (2001) demonstrated that frequently repetitive retrieval inhibition led to the negative control effect. This voluntary memory suppression was associated with increased activity in the dorsolateral prefrontal cortex (DLPFC) and anterior cingulate cortex (ACC) and with decreased

* Corresponding authors.
E-mail addresses: liuchao@bnu.edu.cn (C. Liu), luoyj@bnu.edu.cn (Y.-J. Luo).

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http://dx.doi.org/10.1016/j.neuropsychologia.2012.08.004

activity in the hippocampus (Anderson et al., 2004). This fronto-hippocampal modulation supported the notion that memory suppression is mediated by down-regulation of mnemonic processing in the hippocampus via an executive inhibitory control operated by the frontoparietal network (Anderson & Huddleston, 2012; Anderson et al., 2004). Moreover, behavior, neuropsychological, and brain imaging studies in health and diseases also suggest that early attention plays a critical role in memory suppression most likely through its modulatory effects on executive and memory processing. For instance, the negative control effect is influenced by several factors such as age (Anderson, Reinholz, Kuhl, & Mayr, 2011), depression (Joormann, Hertel, Brozovich, & Gotlib, 2005), and executive ability (Joormann, Hertel, LeMoult, & Gotlib, 2009; Levy & Anderson, 2008). During memory suppression, the activated control-related regions were also engaged in stopping motor action task, which supports the idea that stopping memory retrieval and overriding prepotent action may share a similar neural mechanism (Anderson & Weaver, 2009). For example, ADHD individuals with inhibitory difficulties in both motor response and memory retrieval showed reduced activity in the right lateral prefrontal cortex (rLPFC) relative to control individuals (Anderson & Huddleston, 2012; Depue, Burgess, Willcutt, Ruzic, & Banich, 2010). In sum, memory suppression is mediated by a chain of multiple cognitive processes, including visual processing, attention reallocation, executive, and inhibitory control.

As a technique with high temporal resolution, ERPs have also been used to investigate neurocognitive processes underlying memory suppression with the T/NT paradigm (Bergström, de Fockert, & Richardson-Klavehn, 2009a; Bergström, de Fockert, & Richardson-Klavehn, 2009b; Bergström, de Fockert, & Richardson-Klavehn, 2007; Mecklinger, Parra, & Waldhauser, 2009). Several ERP components have been found to be related to memory suppression processing. First, early positive potentials, associated with attention to stimulus characteristics at visual processing stages (Smid, Jakob, & Heinze, 1999), was larger for Think items than it was for No-Think items in T/NT task (Bergström et al., 2007; Mecklinger et al., 2009). Second, Bergström et al. (2009b) found an early N2 component that emerged around 200 ms post-stimulus was temporally similar to the No-Go-N2 potential. It was enhanced for No-Think items vs. Think items and may be associated with inhibitory activity (Anderson et al., 2004; Bergström et al., 2009b; Falkenstein, 2006; Mecklinger et al., 2009; Wessel & Merckelbach, 2006). Third, another inhibition-related later negativity (LN) component emerged at around 300–500 ms post-stimulus with a fronto-central distribution (Bergström et al., 2009b). The magnitude of this LN for No-Think trials was modulated by the direct suppression of memory elicited by the requirement of participants to block memory retrieval of the targets by continuously focusing only on the cues. The LN was larger for subsequently forgotten words than for subsequently remembered words in the T/NT task (Bergström et al., 2009b). Finally, previous studies also reported a parietal episodic memory (EM) effect, which was reflected by a late parietal positivity (LPP) component emerging approximately 400–800 ms after cue onset, which is noted to be associated with conscious recollection (Bergström et al., 2009a, 2009b, 2007; Hanslmayr, Leipold, Pastötter, & Bäuml, 2009; Mecklinger, 2000; Mecklinger et al., 2009; Rugg & Curran, 2007; Rugg, Woodruff, & Hayama, 2006; Rugg & Yonelinas, 2003). The LPP, typically left-lateralized (Friedman & Johnson, 2000; Rugg & Curran, 2007) but sometimes bilaterally distributed (Allan & Rugg, 1997), is sensitive to T/NT manipulation. No-Think items usually elicit a smaller LPP than Think items in the T/NT task (Bergström et al., 2009a, 2009b, 2007; Hanslmayr et al., 2009; Mecklinger et al., 2009). The reduction in this ERP marker is presumably associated with the attenuated recollection-related activity in the hippocampal-parietal cortical network (Anderson et al., 2004; Depue et al., 2007). In the study of Bergström et al. (2009b) the forgotten words elicited larger LN and smaller LPP than remembered words in final test. These results were consistent with the fronto-hippocampal hypotheses that suppressing awareness of unwanted memory engaged prefrontal cortex to exert influence on the activity of hippocampus (Anderson & Huddleston, 2012).

However, most of these previous memory suppression studies use neutral materials. Thus, how people suppress emotional information, especially negative information, remains unclear. Several behavioral studies have examined the voluntary suppression of emotional memory with the T/NT task but the results are inconsistent (Depue et al., 2006; Dieler, Plichta, Dresler, & Fallgatter, 2010; Lambert, Good, & Kirk, 2010). Some researchers have demonstrated that the suppression of emotional information was more effective than the suppression of neutral information (DePrince & Freyd, 2004; Depue et al., 2006; Wessel & Merckelbach, 2006). For example, recollection of negative memories was greater than recollection of neutral memories in the Think condition. The opposite occurred in the No-Think condition, which indicated a facilitation of retrieval inhibition for negative memories (Depue et al., 2006). Lambert et al. (2010) found that memory impairment in the T/NT task was significant for items associated with emotionally negative material but not for memories associated with emotionally positive information. However, other researchers found that the memory suppression effect was not different between negative, positive and neutral words in the T/NT task (Dieler et al., 2010). These discrepancies suggest a complex mechanism involving interplay of multiple neurocognitive processes in determining whether suppression of unwanted emotional memories succeeds.

Conducting fMRI technique in a T/NT task, Depue et al. (2007) found a DLPFC-hippocampal network that suppresses memory retrieval and argued that the suppression of negative memories has two time-differentiated neural mechanisms over repeated blocks in T/NT phase. The first phase is associated with suppression of the regions related to sensory components of memory representation, which is modulated by right inferior frontal gyrus (rIFG). The second phase involves the cognitive control by right medial frontal gyrus (rMFG) over the regions implicated in memory processes and emotional components of memory representation, including hippocampus and amygdala. It suggested that the suppression of emotional memories involved a shift in the mechanisms from the initially suppressing visual imagery occurring in early blocks to suppression of the memory itself occurring in the later blocks. Although Depue and colleagues addressed time effects of repetitive memory suppression, it is still not clear what the specific time course of memory suppression in a millisecond scale of event-related transient processing. Also, Depue et al. (2007) did not include neutral materials as a control in their study so the suppression of negative memories from the suppression of memories could not be distinguished in general. In addition, the strategies that the participants used in T/NT phase were not explicitly controlled or reported. Recently, Butler and James (2010) performed an fMRI study to compare suppression effect of negative vs. neutral words using the attentional distraction strategy. They found a negative correlation between fronto-parietal activation and posterior hippocampus activation for suppression of neutral words but not negative words (Butler & James, 2010). However, in their study only six repetitions of suppression were included and the each repetition lasted only two seconds, unlike the ten repetitions and four seconds usually used in previous studies. Although the above studies divided fMRI data into several runs to investigate the neural differentiation over time, the suppression processes within each trial was not clarified. Due to higher temporal resolution, the ERP may be a better technique to examine such processes. Although several previous ERP studies have focused on the temporal properties of memory suppression (Bergström, et al., 2009a, 2009b; Hanslmayr et al., 2009; Mecklinger et al., 2009; Minnema & Knowlton, 2008) few have taken emotion into account. In a recent study, Hauswald et al. (2011) found that, unlike neutral pictures, highly arousing negative pictures are exempt from directed suppression due to their initial automatic processing, reflected by the LPP component. However, they use a directed forgetting paradigm rather than a T/NT task, and thus it cannot directly reflect retrieval suppression.

The primary focus of the current study was to investigate the specific time course of negative memory suppression in the T/NT task using the ERP technique. Several inhibitory strategies, including direct suppression and thought substitution, are likely involved in intentional memory suppression. In previous study, in order to draw more general conclusion participants were allowed to use whatever strategy they wished to suppress memories (Anderson & Green, 2001; Anderson et al., 2004; Depue et al., 2007). Instead, in the present study, we use two types of targets in order to eliminate the possibility that the difference in ERPs is due to the different nature of targets or strategies employed by participants. Therefore, a more defined strategy (e.g., direct suppression) is required to draw specific conclusions. Based on the results of previous ERP research, we expected interaction effects between memory suppression and emotion values. Previous studies have provided ERP evidence, an enhanced LPP, that negative memory was recollected to a higher degree than neutral memory, suggesting an emotion-induced memory enhancement of recognition memory (Hauswald et al., 2011; Johansson, Mecklinger, & Treese, 2004). Therefore, we expected that negative memories elicit larger LPP amplitudes than neutral memories in both Think and No-Think conditions. Moreover, studies have suggested that negative information is less easily suppressed (Dolcos, LaBar, & Cabeza, 2004; Dolcos, LaBar, & Cabeza, 2005; Kensinger & Corkin, 2003), so we could expect that the amplitude of the LN component that indexes actual item suppression in the T/NT task (Bergström et al., 2009b) would be smaller for negative memories than for neutral memories in the No-Think condition.

2. Methods

2.1. Participants

Twenty young, healthy right-handed volunteers (12 females; Mean age = 21.63 years), with normal or corrected-to-normal vision, participated in the experiment. All reported no history of neurological or psychiatric disorders. Four participants' data were discarded from analysis, because of excessive movement artifacts. The written informed consent was collected in accordance with the Institutional Review Board (IRB) at the Institute of Psychology of the Chinese Academy of Sciences.

2.2. Stimuli

The Think/No-Think paradigm was performed using face-picture pairs (Depue et al., 2007). Forty-eight female faces previously rated as having a neutral expression by 20 participants in a pilot study (on two separate 9-point scales, 1 = "extremely sad" or "not arousing at all" whereas 9 = "extremely happy" or "extremely arousing", mean valence = 5.29 ± 0.93, mean arousal = 5.13 ± 0.79) were used as cues. Forty-eight target pictures were selected from the international affective picture series (IAPS) (Lang, Bradley, & Cuthbert, 2008). Half the pictures were negative and half were neutral in emotional content. The negative target pictures differed from neutral target pictures in valence (2.69 vs. 5.45, $t_{(46)} = -12.75$, $P < 0.001$),but not in arousal (5.64 vs. 5.23, $t_{(46)} = 1.90$, $P = 0.12$). All pictures were presented against a white background with identical size and resolution (visual angles of 7.2° (vertical) and 10.7° (horizontal), 100 pixels per inch) in a CRT display with a 100 Hz refresh rate. Participants viewed the stimuli from a distance of approximately 80 cm in a quiet, electrically shielded room.

2.3. Procedure

The experimental procedure was divided into three phases (see Fig. 1): the training, T/NT, and test phases (Depue et al., 2007). In the training phase, participants learned to remember 48 face-picture pairs displayed side by side for 4000 ms. In order to test the training effect, we conducted a recognition task in which participants were shown two pictures and a face and were asked to select which of the two pictures had been originally paired with that face. All the face cues have been presented beforehand in the training phase. This procedure continued until participants were able to identify the correct pair with 95% accuracy (mean times = 3.56) over all 48 face-picture pairs. **The recall accuracy for negative items did not differ from the neutral items (Mean accuracy = 95.8% and 96.3%, respectively, *P* = 0.12)**.

In the T/NT phase, participants were instructed to use the face as a memory cue to recall (Think condition) or inhibit (No-Think condition) the associated picture according to the color of a border around the face: green for Think trials and red for No-Think trials. Each trial consisted of a face with a red or green border of 3500 ms, and then a 500 ms inter-trial interval. Only 32 of the 48 faces were presented in the T/NT phase with 10 repetitions: 16 had been paired with neutral pictures and the other 16 had been paired with negative pictures, with half for Think and half for No-Think trials. The remaining 16 faces served as the baseline and were not presented in this phase. Therefore, 320 critical trials were equally separated into four stimuli types depending on the pictures' emotionality and the memory manipulation task: Neutral Think, Neutral No-Think, Negative Think and Negative No-Think. For the Think trials, participants were told, "Try your best to recall the picture initially paired with the face and keep it in mind." Similar to the direct suppression instruction used in study of Bergström et al. (2009b), for the No-Think trials participants were told, "Prevent the previously associated picture from entering consciousness." In order to obtain an ideal suppression effect, participants were instructed to pay full attention to the cue and not to think of anything else. No overt responses were required. The electroencephalograms (EEG) were recorded during this phase.

In the test phase, we followed the task used in study of Depue et al., (2007) to show faces and require the participants to produce a description of 3–5 words for the pictures associated with the faces. These descriptions were then recorded and rated by two independent experimenters to provide the recall accuracy (1 for correct and 0 for incorrect) (inter-rater reliability was 0.98). During this phase, all 48 faces were presented, including 32 faces (neutral and negative associates) that had been

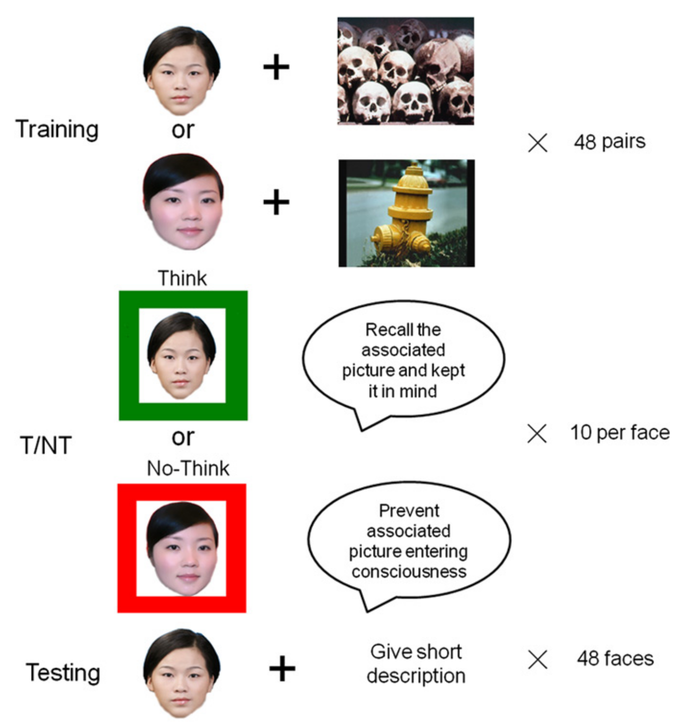

Fig. 1. Illustration of the experimental procedure. First, participants were trained to associate 48 cue-target pairs. Then, the EEG was recorded while participants viewed only the face (32 faces, 8 faces per condition, 10 repetitions per face) during the T/NT phase. Pictures were framed in the green color cue for Think trials and in the red color cue for No-Think trials. Finally, during the test phase, each individual was shown one of the 48 faces and asked to describe its associated pair. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

presented in the T/NT phase and 16 (baseline) that had not been presented in the T/NT phase. After the test, participants were asked to explain the strategy that they had adopted in the No-Think task. All participants reported that they had tried their best to suppress any information after seeing the No-Think cues.

2.4. ERP recording

The EEG was recorded using the NeuroScan recording system with 64-channel scalp electrodes, online reference to the left mastoid and off-line algebraic re-reference to the average of the left and right mastoids. The distribution of electrodes was set according to the international standard 10–20 sites system. The vertical electrooculogram (EOG) was recorded supra- and infra-orbitally at the left eye and the horizontal EOG was recorded from the left vs. the right orbital rim. The impedances of all electrodes were kept below 5 kΩ. EEG and EOG signals were filtered with a 0.05–100 Hz bandpass filter and continuously sampled at 500 Hz/channel.

We analyzed ERP signals time-locked to the presentation of the face cue in the T/NT phase. Trials with peak-to-peak deflection exceeding ±50 μV were excluded from averaging. A 30 (24 db/oct) Hz low pass filter was applied offline. ERP data were computed using a 1200 ms epoch locked to the onset of face stimuli with a prestimulus baseline of 200 ms. This led to an average of 61 (ranging from 52 to 74), 62 (ranging from 53 to 76), 58 (ranging from 48 to 70) and 63 (ranging from 50 to 77) artifact-free trials for the four conditions: Neutral Think, Neutral No-think, Negative Think, and Negative No-think, respectively. The trial numbers are not significantly different across these four conditions.

2.5. ERP analysis and statistics

The ERP data were analyzed using NeuroScan EDIT software (Version 4.3). According to the previous studies on memory suppression (Bergström et al., 2009b; Mecklinger et al., 2009) and an inspection of the grand-averaged waveforms, we focused our analyses on four ERP components: P1, N2, LN and LPP. The baseline-to-peak amplitudes and latencies were measured for P1, N2 and LN whereas mean amplitudes were measured for LPP. Electrodes with maximal amplitude over all conditions were selected for statistical analysis. We analyzed the P1 component (70–140 ms) at the PO3, PO*z*, PO4, O1, O*z* and O2 electrodes, N2 (150–260 ms) and LN (380–500 ms) components at the F3, F*z*, F4, FC3, FC*z* and FC4 electrodes and the LPP (500–800 ms) component at the C3, C*z*, C4, P3, P*z* and P4 electrodes.

Statistical analyses with the repeated-measure ANOVA with multiple pairwise comparisons were conducted on the amplitude and latency of P1, N2 and LN, as well as the mean amplitude of LPP. ANOVA factors were valence (negative vs. neutral), T/NT (Think vs. No-Think) and Electrode sites. All the *P* values of main effects and interactions in both behavioral and ERP data were corrected using the Greenhouse–Geisser method.

2.6. ERP source analysis

In order to confirm the differential brain areas involved in negative memory suppression, source localization was performed by means of sLORETA (standard Low Resolution Elecromagnetic Tomography), which provides localization by computing the smoothest cortical current density distribution (Pascual-Marqui, 2002). Computations were made in a realistic head model (Fuchs, Kastner, Wagner, Hawes, & Ebersole, 2002), using the MNI152 template (Mazziotta et al., 2001), with the three-dimensional solution space restricted to cortical gray matter. Anatomical labels as Brodmann areas are reported using an appropriate correction from MNI to Talairach space (Brett, Johnsrude, & Owen, 2002). Thus, sLORETA images represent the electric activity at each voxel in neuroanatomic Talairach space (Talairach & Tournoux, 1988) as the squared standardized magnitude of the estimated current density.

The sLORETA analyses were conducted on the grand-averaged ERP difference waves of P1 (70–140 ms), N2 (150–260 ms), and LPP (500–800 ms) between the Think and No-Think conditions as well as the grand-averaged ERP difference waves of LN (380–500 ms) and LPP (500–800 ms) between the negative and neutral memories in the No-Think conditions. In order to identify the brain electrical activity accurately, an average reference was used. Paired comparisons were performed for each voxel using statistical non-parametric mapping (Holmes, Blair, Watson, & Ford, 1996). The results correspond to maps of log-*F*-ratio statistics for each voxel, for corrected $P<0.05$ (Pascual-Marqui, 2002).

3. Results

3.1. Behavior results

We calculated recall accuracy of Think, No-Think and baseline for both neutral and negative pictures. The data were then submitted to a 2-by-3 repeated-measure analysis of variance (ANOVA) with valence (negative vs. neutral) and T/NT (Think, No-Think and baseline) as factors. The results showed a significant main effect of T/NT (Think, No-Think and baseline), F (2, 30)=48.62, $P<0.001$, $\eta^2=0.76$, such that the Think condition received higher recall accuracy than the No-Think condition ($P<0.001$) and baseline ($P<0.001$), and No-Think condition had lower recall accuracy than baseline ($P<0.001$). We also found a significant valence × T/NT interaction, F (2, 30)=7.46, $P<0.01$, $\eta^2=0.33$, such that negative pictures received higher recall accuracy than neutral pictures in the No-Think condition ($P<0.05$). For neutral pictures, the Think condition received higher recall accuracy than the No-Think condition ($P<0.001$) and baseline ($P<0.001$), and No-Think condition had lower recall accuracy than baseline ($P<0.001$). For negative pictures, the No-Think condition received lower recall accuracy than the Think condition ($P<0.01$) and baseline ($P<0.05$), and the Think condition had marginally higher recall accuracy than baseline ($P=0.061$). No significant differences were found between negative and neutral pictures in the Think condition ($P=0.49$). No significant differences were found between the two baseline conditions ($P=0.14$) (see Table 1 and Fig. 2). **To examine the valence effect on below-baseline forgetting, we conducted an ANOVA only with valence (negative vs. neutral) and NT/baseline (No-Think and baseline) as factors. The results showed a marginally significant valence × T/NT interaction, F (1, 15)=3.64, $P=0.076$, $\eta^2=0.20$. Negative pictures received higher recall accuracy than neutral pictures in the No-Think condition ($P<0.05$), but no differences were found in recall accuracy between negative and neutral pictures in the baseline condition ($P=0.14$). Baseline received higher recall accuracy than the No-Think condition for both negative ($P<0.01$) and neutral pictures ($P<0.01$)**. Consistent with previous studies, for both neutral and negative information, the repetitive presentations of Think trials led to enhanced recall accuracy and the repetition of No-Think trials resulted in declined recall accuracy (Anderson & Green, 2001; Anderson et al., 2004; Depue et al., 2006, 2007). The negative pictures were more difficult to be suppressed than neutral ones, although we found the negative control effect for both.

3.2. ERP results

Fig. 3 shows grand-averaged ERPs elicited by faces associated with negative and neutral pictures under the Think and No-Think conditions. Four ERP components, P1, N2, LN and LPP, were analyzed in the present study.

3.2.1. P1

P1 amplitudes showed only a significant main effect of T/NT condition, F (1,15)=9.48, $P<0.01$, $\eta^2=0.39$.The amplitude of P1 in Think condition (*Mean*=5.34 μV) is larger than that in No-Think condition (*Mean*=4.37 μV). No significant main effects and interaction were found for the P1 latency.

Table 1
The mean (with SD) recall accuracy of Think, No-Think and baseline by valence. All the recall accuracy recorded in the test phase was calculated.

	Negative	Neutral
Think	66.6(23.0)	72.2(20.9)
No-Think	44.8(17.6)	30.8(18.5)
Baseline	55.6(10.2)	49.5(14.7)

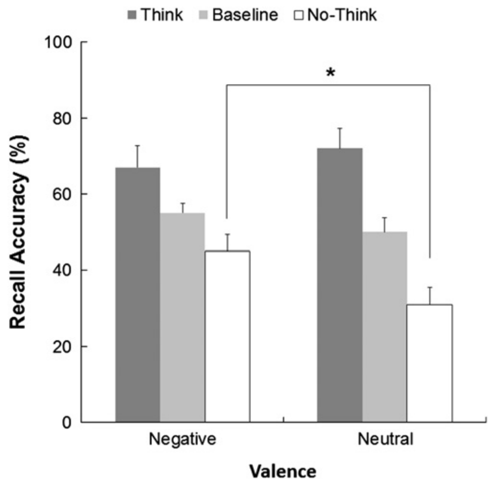

Fig. 2. Bar plot showing recall accuracy of Think, No-Think and baseline conditions for both negative and neutral pictures. There was a significant main effect of T/NT (Think, No-Think and baseline), $F(2, 30)=48.62$, $P<0.001$, $\eta^2=0.76$, such that the Think condition received higher recall accuracy than the No-Think condition ($P<0.001$) and baseline ($P<0.001$), and No-Think condition had lower recall accuracy than baseline ($P<0.001$). There was a significant interaction ($P<0.01$), such that negative pictures received a higher recall accuracy than neutral pictures in the No-Think condition ($P<0.05$). No significant difference was found between negative and neutral pictures in the Think condition ($P=0.49$). No significant difference was found between the two baseline conditions ($P=0.14$). *$P<0.05$.

3.2.2. N2

N2 amplitudes showed only a significant main effect of T/NT, $F(1,15)=8.63$, $P<0.05$, $\eta^2=0.37$, such that the No-Think condition (*Mean*=0.03 μV) showed a larger N2 amplitude than Think condition (*Mean*=1.13 μV). No significant main effects and interactions were found for the N2 latency.

3.2.3. LN

LN amplitudes showed a significant main effect of T/NT condition, $F(1,15)=21.30$, $P<0.001$, $\eta^2=0.59$, and a significant valence × T/NT interaction, $F(1, 15)=4.59$, $P<0.05$, $\eta^2=0.23$.Separate analysis for the factor of T/NT revealed that negative memories elicited a smaller LN amplitude than neutral memories did in the No-Think condition (0.46 μV vs. –0.77 μV, $P<0.05$, $\eta^2=0.29$) but not in the Think condition. A separate analysis for the factor of valence revealed that the No-Think condition (*Mean*=0.46, −0.77 μV, $P<0.01$, $\eta^2=0.41$) had a larger LN amplitude than the Think condition had (*Mean*=1.42, 1.85 μV, $P<0.01$, $\eta^2=0.47$) for both negative and neutral memories. No significant main effects and interactions were found for the LN latency.

3.2.4. LPP

LPP amplitudes showed a significant main effect of T/NT, $F(1, 15)=23.32$, $P<0.001$, $\eta^2=0.61$, and a significant valence × T/NT interaction, $F(1, 15)=7.18$, $P<0.05$, $\eta^2=0.32$. Separate analysis for the factor of valence revealed that the Think condition (*Mean*=4.58, 4.94 μV, $P<0.01$, $\eta^2=0.51$) had a larger amplitude than the No-Think condition had (*Mean*=3.00, 2.41 μV, $P<0.001$, $\eta^2=0.62$) for both negative and neutral memories. In order to investigate the emotional effect in the No-Think condition, a repeated-measure ANOVA was conducted with valence and electrode sites. The valence × electrode sites interaction for LPP were significant in the No-Think condition, $F(5, 75)=3.81$, $P<0.01$, $\eta^2=0.20$. Further analyses revealed significant valence effects only in the No-Think condition at C3 ($F(1, 15)=6.13$, $P<0.05$, $\eta^2=0.29$) and P3 ($F(1, 15)=7.47$, $P<0.05$, $\eta^2=0.33$) sites, such that negative memories (*Mean*=3.99, 3.18 μV) had larger LPP than neutral memories (*Mean*=2.86, 2.32 μV). However, in the Think condition there was no significant valence × electrode sites interaction, $F(5, 75)=0.37$, $P=0.71$.

3.3. Electrophysiological source analysis results

The sLORETA results (see Fig. 4 and Table 2) indicate the differences in estimated current density on the basis of grand-averaged ERP difference waves of P1, N2, LN, and LPP. The P1 difference wave (Think condition minus No-Think condition) yielded maximum current density at the vicinity of the visual area in the occipital lobe, Brodmann area 19 (Talairach coordinates: 20, −91, 28; $t=1.75$). The N2 difference wave (No-Think condition minus Think condition) yielded maximum current density in the right medial frontal gyrus, Brodmann area 11 (Talairach coordinates: 5, 62, −16; $t=1.15$), and right inferior frontal gyrus, Brodmann area 10 (Talairach coordinates: 45, 48, −2; $t=1.11$). Significantly higher estimated current density was observed for neutral No-Think LN than for negative No-Think LN in the right superior frontal gyrus, Brodmann area 11 (Talairach coordinates: 30, 53, −15; $t=2.26$), and right medial frontal gyrus, Brodmann area 11 (Talairach coordinates: 35, 53, −15; $t=2.24$). The sLORETA results also revealed that estimated current density of LPP was significantly higher for Think than for No-Think conditions in parietal regions, Brodmann area 7 (Talairach coordinates: −5, −75, 50; $t=3.92$) and for negative No-Think than for neutral No-Think in the parietal lobe, Brodmann area 7 (Talairach coordinates: −25, −75, 45; $t=1.39$).

4. Discussion

In the present study we examined the time course of emotionally negative and neutral memory suppression. Negative and neutral memories can be suppressed intentionally, but negative memories were more difficult to be suppressed than neutral ones. ERP and source analyses further demonstrated that the suppression of negative memories was associated with significantly smaller LN and a larger LPP, primarily at the right medial and superior frontal gyri. In addition, memory suppression processing generally associated with changes in early components during the time window of 70–260 ms, such as P1 and N2, mainly at the right inferior frontal gyrus and occipital lobe. Memory suppression also associated with changes in late components during a time window of 300–800 ms. Our results replicated and extended previous behavioral and neuroimaging findings on the suppression of negative memory in many aspects.

First, we replicated the behavioral effect of voluntary memory suppression reported by Anderson and Green (2001). The repetitive recall resulted in enhanced memories for response items (positive control effect), whereas retrieval avoidance resulted in impaired memories for suppressed items (negative control effect).The negative control effect for neutral memories was more prominent than those for negative memories.

There are two possibilities behind the effect of negative memory suppression in the T/NT paradigm. One hypothesis is that emotional negative information can be better elaborated into memory (Dolcos et al., 2004, 2005; Kensinger & Corkin, 2003). That is, emotional negative information is salient, more intrusive, and thus more difficult to be suppressed. Another possibility is that greater cognitive control can be exerted over emotional information than over neutral information (Norman, Newman, Detre, & Polyn, 2006). The latter hypothesis was supported by Depue et al. (2006), who reported that the suppression effect would be more robust for negative than for neutral materials. Our findings were consistent with the first hypothesis and was similar

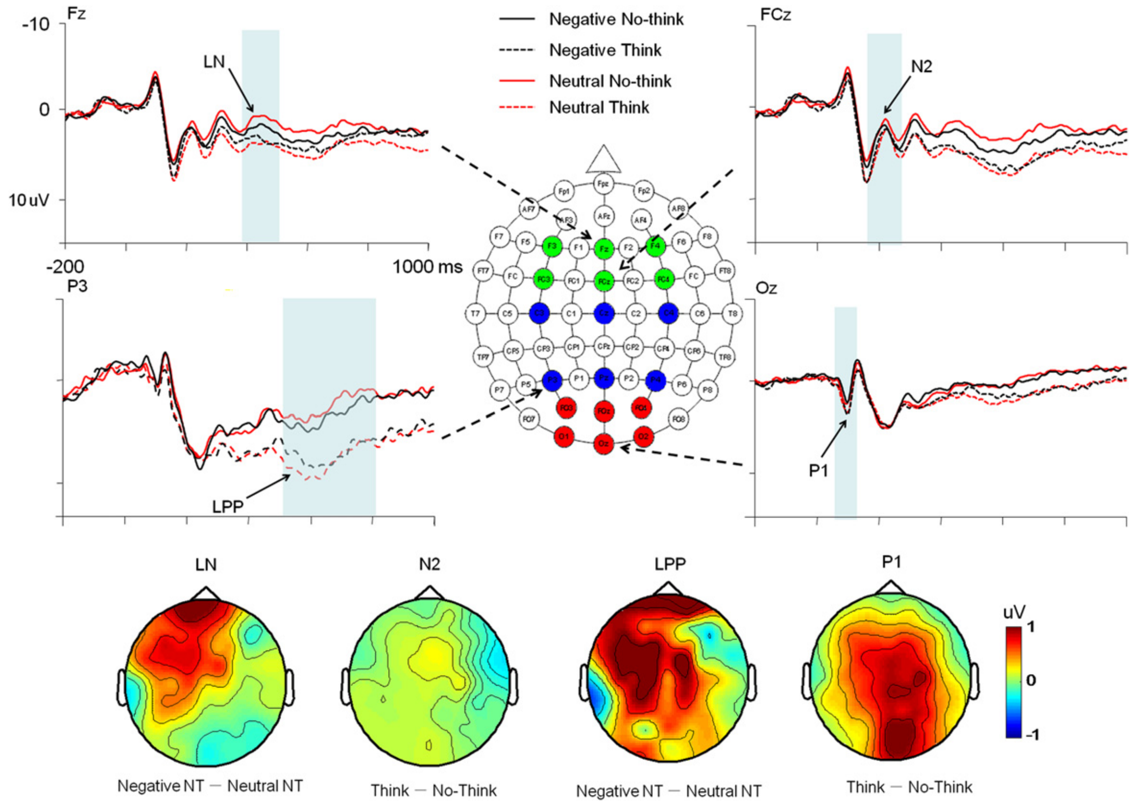

Fig. 3. Grand-averaged ERP waveforms and topographic maps for the four experimental conditions: Negative No-Think, Negative Think, Neutral No-Think and Neutral Think. Electrodes were grouped into three sites in the analysis of different ERP components (as shown in the electrode layout diagram: red for the P1, green for the N2 and later negativity (LN), and blue for the later parietal positivity (LPP).The voltage maps of the difference waves (Think vs. No-Think for P1 and N2; Neutral vs. Negative in No-Think for LN and LPP) for each component (peak for P1, N2 and LN; average for LPP) is shown at the bottom. Generally, Think and No-Think conditions show significant differences in early components over occipital and frontal regions, such as P1 and N2. Contrastingly, negative and neutral memories show significant differences in late components over frontal and parietal regions, such as LN and LPP, only in the No-Think conditions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

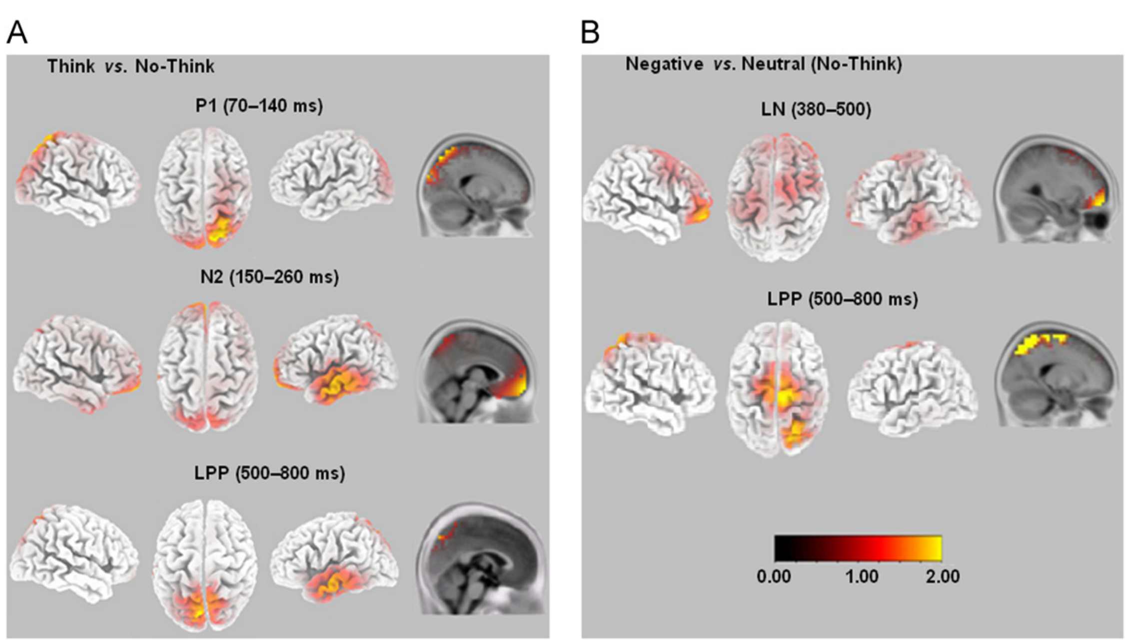

Fig. 4. sLORETA solution for the ERP difference waves of P1, N2, LN and LPP components. The difference wave between the Think and No-Think condition show strong activity at the occipital lobe for P1 in the 70–140 ms time window, at the right medial and inferior frontal gyri for N2 in the 150–260 ms time window, and at the parietal lobe for LPP in the 500–800 ms time window. In contrast, the difference wave between negative and neutral memories in the No-Think condition show strong activity at the right superior and medial frontal gyri for LN in the 380–500 ms time window and at the parietal lobe for LPP in the 500–800 ms time window. The panel A shows strong estimated current density of P1, N2, and LPP between Think and No-Think conditions and the panel B shows strong estimated current density of LN and LPP between Negative No-Think and Neutral No-Think memories.

Table 2
Location of P1, N2 and LPP in Think vs. No-think condition, and the location of LN and LPP in Neutral No-Think vs. Negative No-Think.

Anatomical regions	Brodmann area	Talairach coordinates (x, y, z)	Log-F-Ratio
(a) P1 time window			
Think > No-Think			
Cuneus	19	(20, −91, 28)	1.75
Superior parietal lobule	7	(15, −60, 63)	1.71
Precuneus	7	(15, −70, 50)	1.68
(b) N2 time window			
No-Think > Think			
Medial frontal gyrus	11	(5, 62, −16)	1.15
Inferior frontal gyrus	10	(45, 48, −2)	1.11
Superior frontal gyrus	11	(5, 63, −12)	1.10
Middle temporal gyrus	21	(−64, −10, −12)	1.02
(c) LPP time window			
Think > No-Think			
Superior parietal lobule	7	(−5, −75, 50)	3.92
Precuneus	19	(−30, −81, 36)	1.77
Cuneus	19	(−30, −86, 32)	1.8
Middle temporal gyrus	21	(−64, −20, −7)	2.17
(d) LN time window			
Neutral No-Think > Negative No-Think			
Superior frontal gyrus	11	(30, 53, −15)	2.26
Middle frontal gyrus	11	(35, 53, −15)	2.24
Inferior frontal gyrus	47	(−10, 50, 43)	1.67
Orbital gyrus	11	(10, 52, −24)	1.45
(e) LPP time window			
Negative No-Think > Neutral No-Think			
Superior parietal lobule	7	(−25, −75, 45)	1.39
Precuneus	19	(−35, −71, 40)	1.37
Superior occipital gyrus	19	(−30, −81, 27)	1.35

to previous findings that negative memory had a better recollection accuracy than that of positive memory under the suppression condition (Joormann et al., 2009; Marx, Marshall, & Castro, 2008).

These findings that negative memory had a greater recall than neutral memory after No-Think training may have two interpretations. One is that both negative and neutral memories are comparably learned at the outset and suppression effect is less effective for negative memory because they are more intrusive. The other interpretation is that negative memories are more rapidly encoded, thus more difficult to be suppressed, because of learning enhanced by emotion. Our behavior data supported the first interpretation because negative and neutral pictures did not differ in the baseline condition, thus also suggested an absence of emotion-enhanced learning for negative pictures. These results suggested that people might be able to suppress negative memories even if suppression was greater for neutral memories.

The ERP results revealed more details about the time course of negative memory suppression. First, we found negative and neutral memories differed in a LN component that peaked at 380–500 ms, which distributed around the frontal-central regions in the No-Think condition, such that negative memories elicited smaller LN amplitudes than neutral memories did. According to Bergström et al. (2009b), the fronto-centrally distributed negativity between 300 and 500 ms predicted subsequent item forgetting and confirmed the actual item suppression. The decreased LN for negative memories in the present study thus indicated that the suppression of negative memories was less efficient than that of neutral memories, because of intrusiveness of emotionally negative information. Another possible yet complementary explanation is that the reduced amplitude of LN for negative memories resulted from the decreased cognitive resources allocated to negative items and disengaged from voluntary control. **Memory retrieval requires significant attentional resources. Since attention was captured by emotional features, few attention resources would be allocated to memory retrieval** (Pessoa, 2009). The sLORETA results showed a strong activity in the right superior frontal gyrus and the right medial frontal gyrus for negative memory suppression. Activity in the right medial frontal gyrus has been found to be associated with the suppression of memory processes and the emotional components of the memory representation in the T/NT task (Depue et al., 2007). Activity in the superior frontal gyrus is thought to reflect higher cognitive functions such as planning, attention shift, motivation, and emotional information processing (Boisgueheneuc et al., 2006; Cutini et al., 2008; Rose et al., 2011). It is possible that less cognitive control was exerted on negative memory compared to neutral memory under the suppression condition.

Second, we found that the amplitude of the LPP was greater for negative memories than for neutral memories in the No-Think condition in the 500–800 ms time window. LPP was an ERP marker of conscious recollection and was sensitive to mere retrieval attempts (Falkenstein, 2006; Friedman & Johnson, 2000). According to previous studies (Anderson et al., 2004; Depue et al., 2006), the reduction in the amplitude of LPP suggests an attenuation of recollection-related activity in the hippocampal-parietal network so is most likely a consequence of successful suppression. For example, Bergström et al. (2009b) reported a reduced LPP for subsequent forgotten No-Think trials but not for the remembered No-Think trials. In the present study, the amplitude of LPP for negative memories was larger than that of neutral memories, which could indicate that the suppression of negative memories was less successful than that of neutral memories, as reflected by the higher recall accuracy in behavioral results. This result is similar to a previous fMRI study that showed that lowered hippocampal activation was observed during the suppression of neutral, but not negative words (Butler & James, 2010). In addition, the LPP has also been thought to reflect the amount of conscious recollection that takes place in response to a stimulus (Rugg & Curran, 2007). Therefore the enhanced LPP for negative memories might also indicate that the amount of conscious recollection of negative memories was greater than that of neutral memories and that negative memories were more likely to be revisited under suppressive circumstances due to its intrusiveness nature.

However, the LPP in response to the negative memory did not significantly differ from response to the neutral memory in this study. Previous research has revealed that compared to recall for neutral memories, recall for negative memories did not necessarily enhance hippocampal activity nor memory performance (Onoda, Okamoto, & Yamawaki, 2009). We did not find a facilitation of negative memory retrieval in Think condition.

sLORETA results showed that response items elicited strong activity in parietal regions relative to suppressed items; negative memory suppression led to increased activity in the parietal lobe compared to neutral memory suppression, which could be associated with an increase of recollection-related neural activity in the hippocampal-parietal network. Altogether, these differences in late ERP components between suppression of neutral and negative memories may reflect a down-regulation of conscious recollection of memory representations supported by prefrontal and parietal network. In turn, this explains why aversive memories were more difficult to be suppressed.

Besides the emotion effect, there were also significant main effects of memory suppression between Think and No-Think conditions in two early ERP components in addition to the two late components. The first early component is the parieto-occipital P1 component with an onset at 70 ms and peak around 100 ms, which was significantly more positive in the Think condition than it was in the No-Think condition. The P1 amplitude is sensitive to attention allocated to task-relevant stimuli in the extra-striate visual cortex (Nieuwenhuis, Yeung, Van Den Wildenberg, & Ridderinkhof, 2003; Pizzagalli et al., 2002). In the current experiment, to enable further retrieval operations, participants were required to selectively pay more attention to the Think items, while paying less attention to the No-Think items to prevent further retrieval processing. The enhanced amplitude of P1 for Think items was associated with increased attention allocation and corresponding strategy selection. We thus speculated that memory suppression was influenced by early attention through its modulatory effects on visual imagery of memory. The sLORETA results indicated a decreased activity in the visual areas of occipital lobe for No-Think trials, which suggested that suppression memory cues attenuated the activity of visual cortex by gating and modulating attention allocated to or away from visual stimuli. The initial pathway of Depue's dual phase account involves reduced activity in regions supporting sensory components of the memory representation (visual cortex, thalamus) that occurred in early blocks (Depue et al., 2007). However, the decreased P1 amplitude for No-Think condition observed within a single trial in the current study was associated with attenuated attention paid towards the to-be-suppressed items and thus modulated memory suppression.

The second early component is a prefrontal N2 component that occurred in the time window of 150–260 ms with larger amplitude in the No-Think condition than the Think condition. According to a previous study (Bergström et al., 2009b), this early No-Think negativity can be interpreted as evidence for the detection of conflict. In fact, the T/NT paradigm is a modification of the Go/No-Go task. Thus, the early No-Think negativity was similar to No-Go-N2 potential, which reflected a detection of response conflict (Carter & van Veen, 2002).

Consistent with previous studies (Depue et al., 2007; Hampshire, Chamberlain, Monti, Duncan, & Owen, 2010), which reported that activation in the right inferior frontal gyrus was associated with inhibition and attentional control, the present sLORETA results showed enhanced activity in the frontal lobe, including the right inferior frontal gyrus, for the No-Think condition. Moreover, the N2 and LN results supported the contention that the "family" of inhibition-related ERP negative waves contained the early and later components, which reflected a dynamic process of cognitive control from conflict detection to actual inhibition (Hanslmayr et al., 2009; Lewis, Lamm, Segalowitz, Stieben, & Zelazo, 2006). In summary, these differences in early components may reflect early stages of suppression processing including visual awareness, attention reallocation, and executive processing.

Put together, unlike the two-phase processing hypothesis proposed by Depue et al. (2007) these results give a more precise and detailed temporal description of negative memory suppression within a single trial. We found that the first memory suppression network among the right inferior frontal gyrus and visual cortex works for the suppression of both negative and neutral memories and is activated at a rather early stage, from 70 to 260 ms. In contrast, the suppression of negative memories was modulated exclusively by the second network among the right superior and medial frontal gyri and parietal lobes at a late stage from 380 to 800 ms. Together, these results suggest that the voluntary suppression of negative memories recruit a late conscious recollection mechanism among the prefrontal and parietal network, which could be dissociated from early visual, attention, and executive control processing among the prefrontal and occipital network that are recruited for both negative and neutral memories.

However, there are also other interpretations to the results. For example, Tomlinson et al. proposed another possible interpretations of the results found in the T/NT paradigm (Huber, Tomlinson, Rieth, & Davelaar, 2010; Tomlinson, Huber, Rieth, & Davelaar, 2009), such that people learn to avoid the target memory by retrieving an alternate response in the No-Think and press-enter conditions. In a study using the T/NT paradigm, Tomlinson et al. (2009) found just as much forgetting in a condition where participants simply had to press the enter key as quickly as possible whenever certain cues appeared during stage two (they were not instructed to suppress for these cues). Furthermore, they found that this was equally true for the independent-cue condition and there were no memory deficits in the no-think or press-enter conditions when recognition testing was used instead of the cued-recall testing. These results suggested that there is no memory suppression. Rather there is learning during the no-think condition and this learning produces retrieval interference that produces forgetting.

All current results could also be interpreted from the learned avoidance account, in which an alternative recovery is learned during the suppression training and competes with the original target. Thus the relative differences in neural activity between conditions might reflect greater learning/retrieval in the think condition or greater inhibition in the no-think condition. Both interpretations are equally viable in explaining the T/NT paradigm of memory suppression and future studies are needed to distinguish them.

Another issue that needs to be taken into account is the learning rates of emotional items in the training phase. According to previous studies, negative items attract more attention and lead to a facilitation in encoding, thus negative information can be elaborated better than neutral items into memory (Dolcos et al., 2004, 2005; Kensinger & Corkin, 2003). In our study, one possibility is that negative items were learned faster than neutral items in the training phase, so reduced recall for suppressed neutral vs. negative memories may just reflect better encoding of the negative items. However, if this is the case, we could have expected over learning for negative items in the training phase when they received those extra presentations, which should inevitably resulted in some differences between negative and neural items in the testing phase without T/NT manipulation. Nonetheless, we did not find such differences between negative items and neutral items neither right after the training phase (Mean accuracy = 95.8% and 96.3%, respectively, $P = 0.12$), nor during the testing phase in the baseline rates (Mean accuracy = 55.6% and 49.5%, respectively, $P = 0.14$). Although there might be ceiling effect in the former, there was not in the latter. Therefore, it is less likely that negative items and neutral items differed in the learning rate during training in our study.

Additional description

Negative pictures consist of the following IAPS slides, 1110, 1274, 1304, 1932, 2205, 2345.1, 2352.2, 2399, 2456, 2490, 2716, 2717, 2730, 2751, 2770, 2780, 2799, 2800, 2810, 3001, 3019, 3022, 3160 and 3225. Neutral pictures consist of the following IAPS slides, 1560, 1908, 7077, 7211, 7240, 7279, 7289, 7402, 7461, 7476, 7496, 7497, 7560, 7620, 7632, 7640, 8065, 8117, 8160, 8191, 8192, 8232, 8280 and 8325.

Acknowledgements

We thank Dr. Shaozheng Qin and Shaw Lacy for their valuable discussions, comments and suggestions on this manuscript. This work was supported by the National Basic Research (973) Program

(2011CB711000), the National Natural Science Foundation of China (NSFC) (91132704, 30930031), the National Key Technologies R & D Program (2009BAI77B01), and the Global Research Initiative Program, National Institutes of Health, USA (1R01TW007897) to YJL, and the NSFC (31170971) to CL.

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