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Neurophysiological correlates of memory illusion in both encoding and retrieval phases

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ABSTRACT

False recognition of a critical lure at retrieval in the Deese–Roediger–McDermott (DRM) paradigm depends on different processing of its corresponding associates in the encoding phase. The current study recorded ERPs in both the encoding and retrieval phases to investigate the neural correlates of differential processing of true and false memories, and the roles of encoding and retrieval in eliciting memory illusion. The ERPs recorded at the study phase were characterized by a smaller N170 component and a larger amplitude late positive component (LPC) for associates that elicited later memory illusion than those that did not elicit later memory illusion. These ERP results suggest that increased active semantic associative processing or a gist representation was established for those items that elicited later memory illusion. This interpretation was supported by the serial-position analysis of the ERPs at encoding. Three ERP components were identified at retrieval. The equal early ERP old/new effects for true and false recognition reflected similar semantic priming. The parietal ERP old/new effect was greater for true than for false recognition, reflecting the recollection processes. A late slow negativity ERP distributed at the parietal and right frontal electrode sites differentiated between true and false recognition. The ERP results confirmed that both encoding and retrieval processes are involved in eliciting false memory. The parietal and frontal distributions of LPC at encoding and the late negativity at retrieval may imply a common neural mechanism in monitoring memory encoding and retrieval.

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1. Introduction

The constructive nature of human memory has been revealed by many empirical and theoretical explorations, and the constructive processes may lead to errors, distortion and illusions (Schacter et al., 1998; Moscovitch, 1995; Squire, 1995). The study of these errors helps to uncover the inner

mechanisms of memory. Many recent studies of false memory have used a procedure originally developed by Deese (1959) and subsequently modified by Roediger and McDermott (1995), which elicits high levels of false recall and false recognition, called the “DRM paradigm”. The DRM paradigm involves presenting lists of words (associates), each of which is highly related to a nonpresented critical item (critical lure). When

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asked to freely recall the lists or to recognize the items on the lists among distracter items, subjects often falsely report that the nonpresented critical lures had been experienced in the earlier study lists.

Two sets of theories have been proposed to explain false recall and false recognition in the DRM paradigm. One set assumes that the false memory effects are rooted in encoding, whereas the other considers that these effects arise during retrieval. A typical example of the encoding theories is the implicit-associative response. Underwood (1965) proposed that false recognition originates in an implicit associative response during encoding. For example, when a participant reads the word “nurse”, he/she may think of an associate “doctor”. Later, if the word “doctor” is presented as a lure, the participant may falsely recognize its occurrence in the list because of the earlier implicit associative response. Activation may spread through an associative network so that false-recognition errors arise through residual activation.

Alternatively, the retrieval theories suggest that retrieval processes contribute significantly to the false recall and false recognition phenomena. The contribution of retrieval in eliciting false memory may also be found in some models of memory, in which recognition judgments are based on the global similarity between studied and tested items (e.g., Arndt and Hirshman, 1998; Clark and Gronlund, 1996). The “familiarity” component of dual-process theories of recognition memory is thought to be based on the computation of global similarity (Hintzman and Curran, 1994; Yonelinas, 1998), whereas “recollection” entails the retrieval of specific information about studied items, such as physical attributes or associative, contextual or source information (Curran and Cleary, 2003).

Another possibility is that false memory of the critical lure reflects the combined processes of encoding and retrieval. McDermott and Watson (2001) proposed a dual-process (activation-monitoring) model to account for their own findings and those of others. Besides emphasizing the activation processes, they put forward the importance of “monitoring” processes, a much more strategic, controlled process or set of processes that can influence whether activation triggers a later false memory. Like activation, monitoring can occur during encoding or retrieval. During encoding, monitoring concerns the differentiation between what occurs in the environment and the thoughts aroused by external events. During retrieval, monitoring involves processes such as disentangling prior thoughts from prior overt experience. Thus, both encoding and retrieval processes may contribute to the false memory of the critical lure.

This study used event-related potentials (ERPs) to investigate the neural mechanism underlying false recognition in the DRM paradigm. The ERP method provides a moment-by-moment record of relevant neurophysiological activity at the encoding and retrieval phases (Rugg and Coles, 1995), allowing one to explore whether encoding, retrieval or both play a role in eliciting false recognition. As the dual-process (activation-monitoring) model (McDermott and Watson, 2001) proposed, failure of monitoring during encoding, retrieval or both phases would lead to a later false recognition. This study was designed to find neural correlates of false recognition in both encoding and retrieval phases.

Several recent studies have found differences in the neural correlates of true and false memories using positron emission tomography (PET) (Schacter et al., 1996b), functional magnetic resonance imaging (fMRI) (Schacter et al., 1997) and ERPs (Curran and Cleary, 2003; Curran and Friedman, 2004; Curran et al., 2001; Nessler and Mecklinger, 2003; Nessler et al., 2001). Recent ERP studies of false recognition have identified three ERP components. The first is an N400-like component (300–500 ms) that is more negative for new words than for lures or studied words (new>lure=studied); this equal early frontal medial old/new ERP effect for true and false recognition reflects similar familiarity processes. This 300–500-ms familiarity-sensitive component has been called the “FN400” (Curran, 1999, 2000) because of its similarity to the N400 component related to semantic processing (Bentin et al., 1995; Kutas and Federmeier, 2000), but is more frontally distributed. The second ERP component is a parietal component (400–800 ms) that is more positive for true than for false recognition (studied>lure=new), suggesting more-active recollection of perceptual details. This 400–800-ms recollection-related ERP effect has been called the “parietal old/new effect” (Allan et al., 1998; Rugg et al., 1998a; Wilding, 2000; Wilding and Rugg, 1996). The third ERP component is a late, frontally based component (800–2000 ms) thought to reflect post-retrieval processing when the contents of memory must be evaluated for particular features, source information and other details (Allan et al., 1998; Curran and Cleary, 2003; Curran et al., 2001; Nessler et al., 2001; Ranganath and Paller, 2000; Wilding, 1999; Wilding and Rugg, 1996).

Almost all of these ERP studies on false recognition have focused on brain activities recorded during the retrieval phase. However, whether a critical lure is falsely recognized at retrieval should depend upon the different processing of its corresponding associates at encoding. To examine the role of encoding of associates in triggering false recognition of the corresponding critical lure, we recorded ERPs for associates in the study phase and analyzed these according to whether their corresponding critical lures were later falsely recognized. Such effects, often termed “Dm effects” as an abbreviation for ERP “differences” based on later “memory” performance, have been observed in a number of studies (e.g., Friedman and Trott, 2000; Van Petten and Senkfor, 1996). Typically, accurately remembered study-phase items elicit a more positive ERP than do the forgotten items. We expected that more active semantic processing for associates in the study phase and the formation of gist representation of a study list would cause the corresponding critical lure to be falsely recognized during the memory test. Accordingly, we sought to uncover ERP differences at encoding between the two types of associates classified according to whether their corresponding critical lure was later falsely recognized. We proposed that a list of semantically associated words would elicit the memory illusion of the corresponding lure in a manner dependent on the level of activation in the relevant associative network. We hypothesized that presenting more associates serially in a list should gradually increase the activation for the corresponding lure. The increasing activation for the lure should establish a gist representation of the study list, which would also increase the activation elicited by the several following associated words. To test this hypothesis, we compared the ERPs for

associates at earlier serial positions and the ERPs for associates at late serial positions between two conditions classified according to whether they elicited the later false recognition of the corresponding lures. We predicted that the ERP differences between two conditions would be greater at the later than earlier serial positions.

The relationship between encoding- and retrieval-related ERP activities also remains an open issue. Few studies have reported such a comparison, especially in the DRM paradigm. Gonsalves and Paller (2000) recorded ERPs in both the encoding and the retrieval phases to explore the neural correlates of the differences in processing between true and false memories in a reality-monitoring protocol. Another objective of our study was to examine temporal and topographical similarities and differences between the study- and test-phase ERPs to identify the roles of the encoding and retrieval processes in eliciting memory illusion.

2. Results

2.1. Behavioral results

The proportions of “old” and “new” responses to the three item types (old, lure and new items) and mean reaction times are presented in Table 1.

The proportion of old responses was higher for old items than for lure items [$t(19)=4.55$, $p<0.0005$], and higher for lure items than for new items [$t(19)=18.64$, $p<0.0005$]. The reaction times did not differ between the old items given old responses (true recognition), lure items given old responses (false recognition) and new items given new responses (correct rejection).

2.2. ERP results

2.2.1. Study phase (encoding)

The ERPs recorded during the study phase were computed according to whether the corresponding lure was or was not recognized later. Whether the studied associate was correctly recognized or not was not considered in the analysis, as it was hypothesized that all the sequentially presented associates within a study list contributed to the formation of

the gist representation which would cause the false recognition of the corresponding critical lure during the memory test. Participants’ responses to associates in the study phase were classified as “eliciting memory illusion” if participants later incorrectly recognized their corresponding critical lures, or “not eliciting memory illusion” if participants later correctly rejected their corresponding critical lures. The encoding ERPs were compared between two conditions: eliciting memory illusion vs. not eliciting memory illusion. To avoid missing any potential differences, the recording epoch from the stimulus onset to the end of the epoch was divided into 75 consecutive intervals of 20 ms each, and the mean amplitude for each interval was calculated in each condition. For each interval, pairwise t tests were used to compare the two conditions at each electrode. Significant differences in three successive intervals were considered a valid difference. As a result, we identified two components: the occipital N170 between 160 and 220 ms and a broadly distributed “late positive component” (LPC) between 500 and 640 ms (Fig. 1).

2.2.1.1. N170. The N170 peaked 172 ms (Oz) after the stimulus onset and was distributed at the occipital electrode sites. We measured the mean peak amplitude of the N170 between 160 ms and 220 ms. ANOVA was used to assess the effects of condition (whether memory illusion was or was not elicited) and electrode site (O1, O2, OZ) on the mean peak amplitude of the N170. There was a significant main effect of condition [$F(1,19)=15.285$, $p<0.05$] and no significant interaction of condition and electrode site. This result confirmed that the mean peak amplitude of N170 at the occipital electrodes was larger for associates not eliciting memory illusion than for those eliciting memory illusion (Fig. 2).

2.2.1.2. Late positive component. The LPC starting about 400 ms after the stimulus onset peaked at 500–560 ms, and showed a posterior topography with posterior>frontal. To best capture the differences in the LPC between the two conditions, we measured the mean peak amplitude of the LPC between 500 and 560 ms. Three-way ANOVA of the effects of condition \times location (frontal, central frontal, central, central parietal, parietal) \times hemisphere (right, middle, left) showed a significant main effect of condition [$F(1,19)=5.11$, $p<0.05$] and a significant condition \times hemisphere interaction [$F(2,38)=5.62$, $p<0.01$]. This result confirmed that the positive deflection of the LPC was greater for associates eliciting memory illusion than for associates not eliciting memory illusion. The simple main effect of condition was significant over the left hemispheric electrode sites [$F(1,19)=7.13$, $p<0.05$] and the midline electrode sites [$F(1,19)=9.42$, $p<0.01$] (see Table 2 and Fig. 2 for more detail).

2.2.1.3. Serial-position analysis. To test the gist representation hypothesis, we performed a serial-position analysis. We defined two parts in each study list. The early part included the first three serial positions (positions 1, 2 and 3), and the late part included the last three serial positions (positions 5, 6 and 7). The ERPs for associates were averaged within each part.

Table 1 – Behavioral data in the memory test

	Response	
	Old	New
<i>Proportion of responses</i>		
Old	0.74 \pm 0.02	0.26 \pm 0.02
Lure	0.63 \pm 0.03	0.37 \pm 0.03
New	0.12 \pm 0.02	0.88 \pm 0.02
<i>Response time (ms)</i>		
Old	737 \pm 22	811 \pm 32
Lure	754 \pm 27	830 \pm 37
New	812 \pm 35	742 \pm 27

Values are mean \pm SEM.

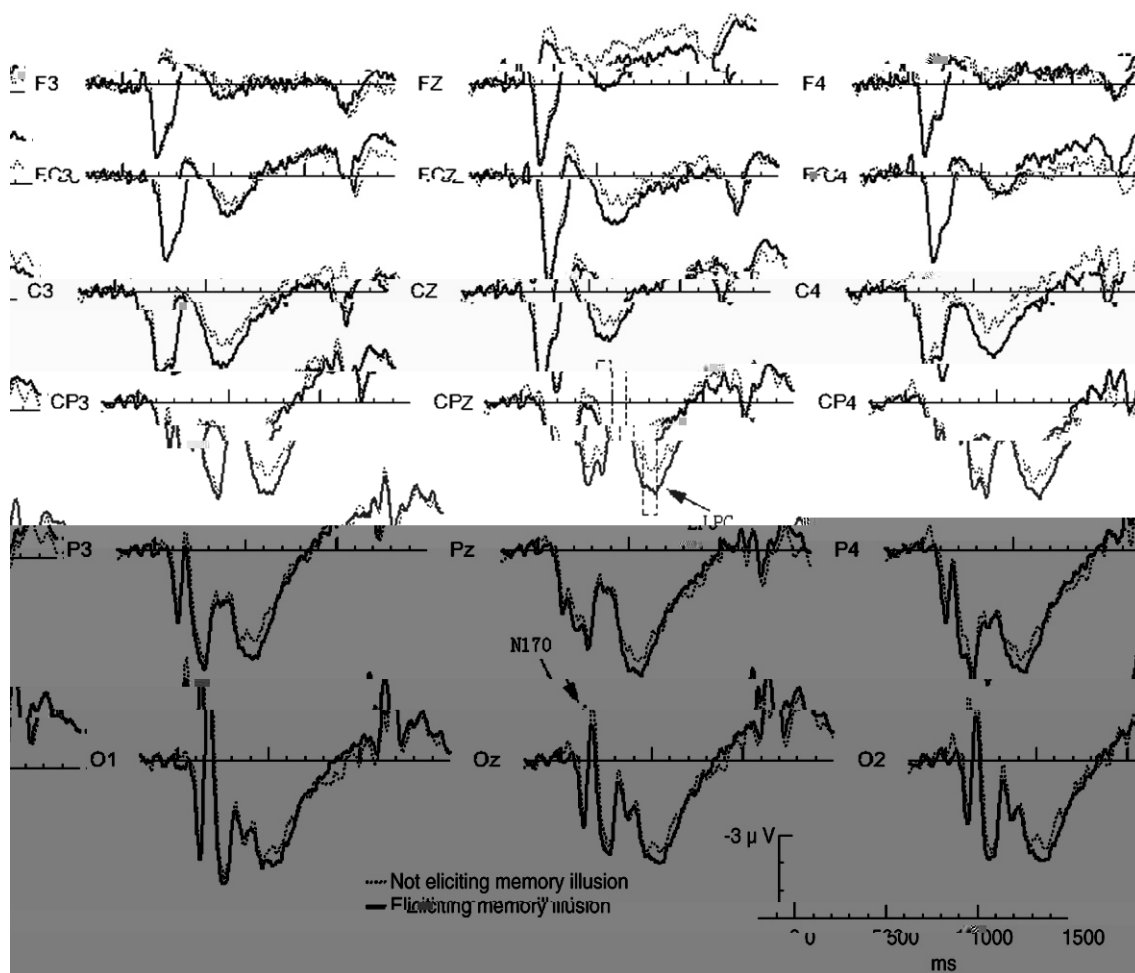


Fig. 1 – ERPs for the main comparisons in the study phase. Voltage is in microvolts, as a function of time in milliseconds (time 0, word onset).

Fig. 3a shows the N170 differences between the two conditions in the early and late parts. In the early part, the mean peak amplitude of N170 was similar for the two types of associates at OZ [$t(19) < 1$]. In the late part, the mean peak amplitude of N170 was less negative for associates eliciting memory illusion than for those not eliciting memory illusion at OZ [$t(19) = 2.23$, $p < 0.05$].

Fig. 3b shows the LPC differences between the two conditions in the early and late parts. In the early part, the mean peak amplitude of the LPC did not differ significantly

between the two types of associates. In the late part, associates eliciting memory illusion evoked a more positive LPC than those not eliciting memory illusion. Fig. 3b shows that the difference in the LPC in the late part was widely distributed across the frontal, central and parietal electrodes. To confirm the serial-position effect of the LPC, an ANOVA was performed on the effects of condition, serial position (early and late parts), and mid-line electrode site (FZ, FCZ, CZ, CPZ, PZ). There was a significant main effect for condition [$F(1,19) = 7.29$, $p < 0.05$], and a significant interaction

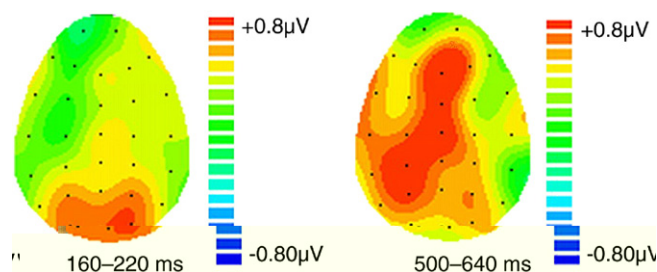


Fig. 2 – Topographic distributions of the ERP differences between associates eliciting memory illusion and those not eliciting memory illusion in the study phase.

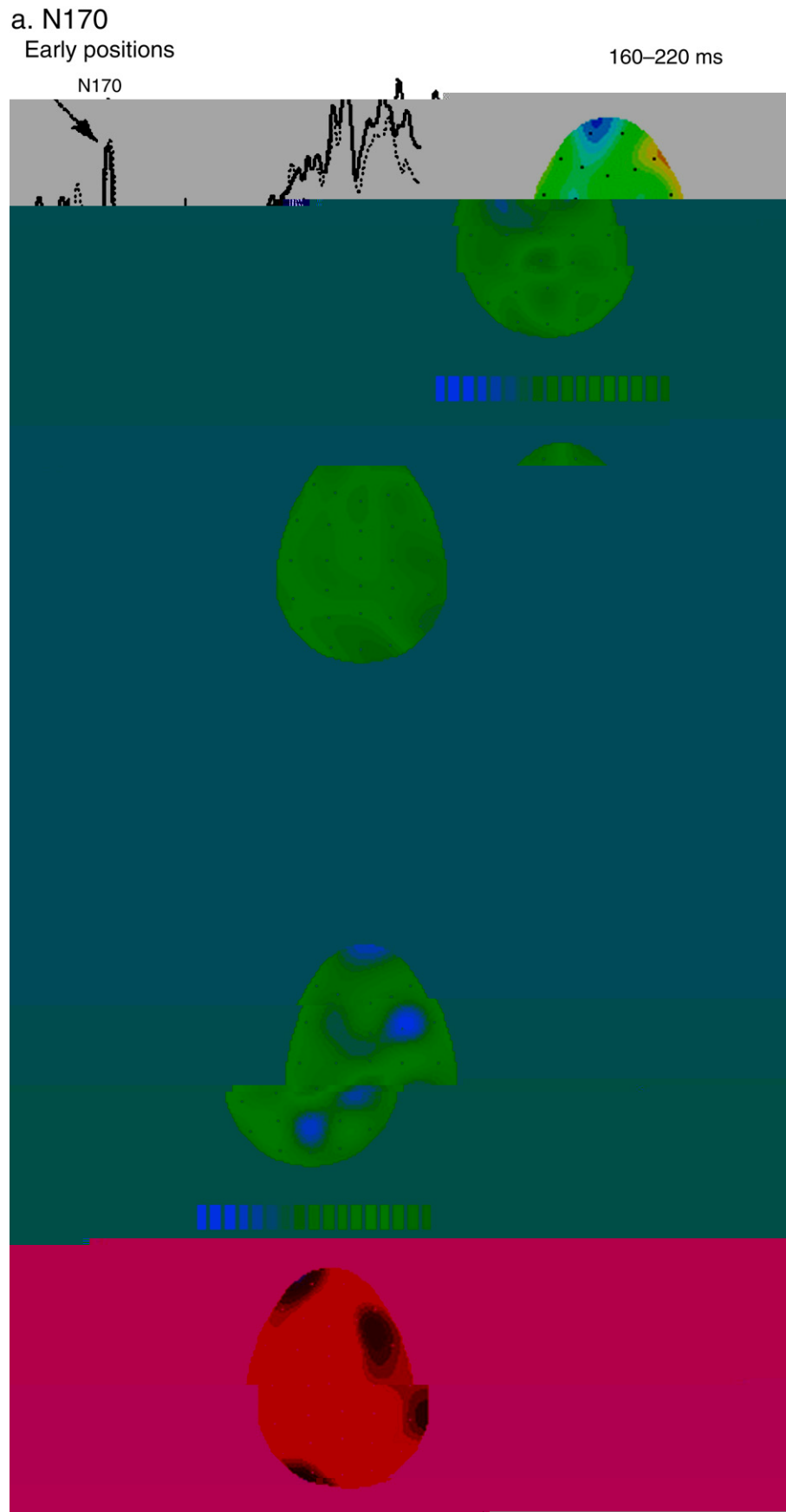


Fig. 3 – ERP waveform differences between two types of associates classified by whether they elicited memory illusion at the different serial positions (left) and the corresponding topographic distributions of the ERP differences (right). (a) N170 effect for the early positions and for the late positions. (b) LPC effect for the early positions and for the late positions.

Table 2 – Mean peak amplitude differences of the LPC (500–560 ms) between two conditions in the study phase

	Left	Middle	Right
Frontal	0.455**	0.902***	0.343
Central frontal	0.451*	0.766*	-0.037
Central	0.613*	0.643*	0.873*
Central parietal	0.780*	0.832*	0.508
Parietal	0.714*	0.535	-0.272

Two conditions were classified by whether memory illusion was or was not elicited. Values represent the difference between the ERP amplitudes measured under conditions eliciting memory illusion minus those not eliciting memory illusion.
Main effect of condition, ANOVA: *** $p < 0.005$; ** $p < 0.01$; * $p < 0.05$.
Electrode regions were: parietal, P3; Pz, P4; central parietal, Cp3; Cpz, Cp4; central, C3; Cz, C4; central frontal, Fc3; Fcz, Fc4; frontal, F3; Fz, F4.

of condition \times serial position [$F(1,19) = 4.90$, $p < 0.05$]. To address the condition \times serial position interaction, we performed simple effect analyses. The effect of condition was significant only in the late part [$F(1,19) = 13.78$, $p < 0.05$]. These results demonstrate that the LPC difference was significant only in the late part.

2.2.2. Test phase (retrieval)

The ERPs recorded in the test phase were computed for true recognition, false recognition and correct rejection (Fig. 4). We selected three different time windows (300–500, 500–700 and

700–1500 ms) to capture the early old/new effect, the parietal old/new effect and the late slow negativity; the mean ERP amplitude was measured over each selected time window. Three-way ANOVA of condition (true recognition, false recognition, correct rejection) \times location (frontal, central frontal, central, central parietal, parietal) \times hemisphere (right, middle, left) was performed in each time window.

2.2.2.1. Early old/new effect (300–500 ms). ANOVA of the effects of condition \times location \times hemisphere showed a significant main effect of condition [$F(2,38) = 12.88$, $p < 0.0005$] and a significant interaction of condition \times location [$F(8,152) = 3.80$, $p < 0.0005$]. The simple main effect of condition was stronger over the posterior than the frontal regions. Bonferroni post hoc tests showed that the amplitudes associated with both true and false recognition were more positive than those linked to correct rejection, whereas the difference between true and false recognition was not significant (see Table 3 for details). These results indicate that the ERPs for true and false recognition reflect equal early old/new effects, but this early old/new effect had a maximal distribution over the central parietal and parietal sites (see Table 3 and Fig. 5), which differs from the frontal distribution observed in other relevant ERP studies (Curran, 2000; Curran and Cleary, 2003; Nessler et al., 2001).

2.2.2.2. Parietal old/new effect (500–700 ms). ANOVA of the effects of condition \times location \times hemisphere revealed only a significant main effect of condition [$F(2,38) = 9.91$, $p < 0.0005$].

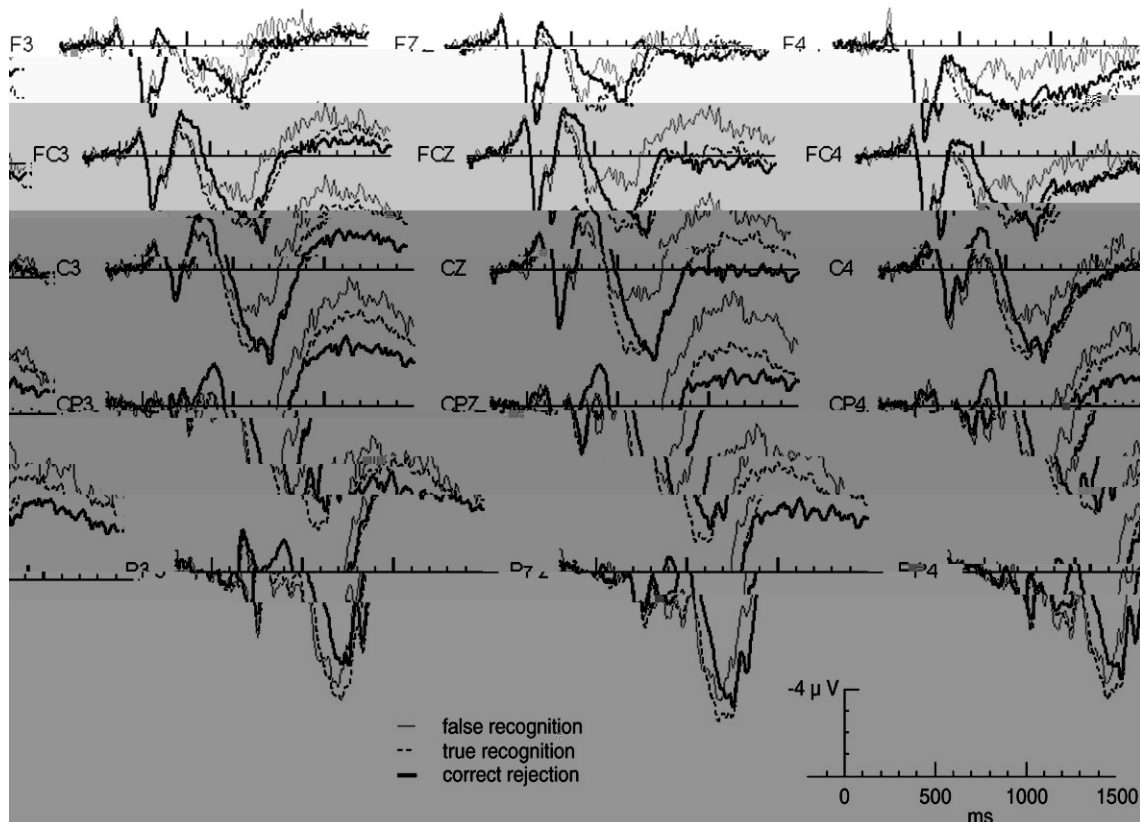


Fig. 4 – ERPs for the main comparisons in the test phase. Voltage is in microvolts, as a function of time in milliseconds (time 0, word onset).

Table 3 – Simple main effect of condition and Bonferroni post hoc analysis between conditions at each location in the test phase (300–500 ms)

	Simple main effect of condition (F(2, 38))	Bonferroni post hoc analysis of mean amplitude differences (μV)		
		TR-CR	FR-CR	TR-FR
Frontal	5.21*	1.04***	0.50	0.46
Central frontal	7.56***	1.18****	0.99*	0.19
Central	9.02***	1.30****	1.12*	0.19
Central parietal	12.09****	1.59****	1.51***	0.08
Parietal	21.10****	1.68****	1.81****	-0.13

Significant level: **** $p < 0.001$, *** $p < 0.005$, ** $p < 0.01$; * $p < 0.05$.
TR, true recognition; FR, false recognition; CR, correct rejection.

Bonferroni post hoc tests showed that true recognition was more positive than both correct rejection (M.D.=0.88, $p < 0.01$) and false recognition (M.D.=1.75, $p < 0.01$), whereas false recognition and correct rejection did not differ significantly (M.D.=-0.87, $p = 0.21$). Similar to data from other studies on false recognition (e.g., Nessler et al., 2001), these results show that true recognition elicited a greater parietal old/new effect than false recognition.

Although the global three-way ANOVA failed to show a significant hemispheric effect, Fig. 5 shows a left-lateralized distribution of the true recognition-correct rejection contrast. To address this hemispheric effect of true recognition vs. correct rejection, we restricted the analyses to the parietal locations. ANOVA of the effects of condition (true recognition vs. correct rejection) × electrode site (P3, PZ, P4) showed a significant main effect of condition [$F(1,19) = 19.54$, $p < 0.0005$] and a significant interaction of condition × electrode site [$F(2,38) = 3.39$, $p < 0.05$]. The simple main effect of condition was larger over the left parietal region [the amplitude difference was 1.61 μV, $F(1,19) = 20.57$, $p < 0.0005$] than over both the middle parietal region [1.05 μV, $F(1,19) = 9.49$, $p < 0.01$] and right parietal region [0.72 μV, $F(1,19) = 7.03$, $p < 0.05$]. The true recognition-correct rejection contrast showed a left-lateralized distribution.

2.2.2.3. Late slow negativity (700–1500 ms). ANOVA of the effects of condition × location × hemisphere showed a significant main effect of condition [$F(2,38) = 8.08$, $p < 0.005$], a significant condition × location interaction [$F(8,152) = 2.52$, $p < 0.05$] and a marginally significant interaction of condition × location × hemisphere [$F(16,304) = 1.55$, $p = 0.08$]. These results suggest that the topographic distribution of the ERP differences was different between the three conditions. To

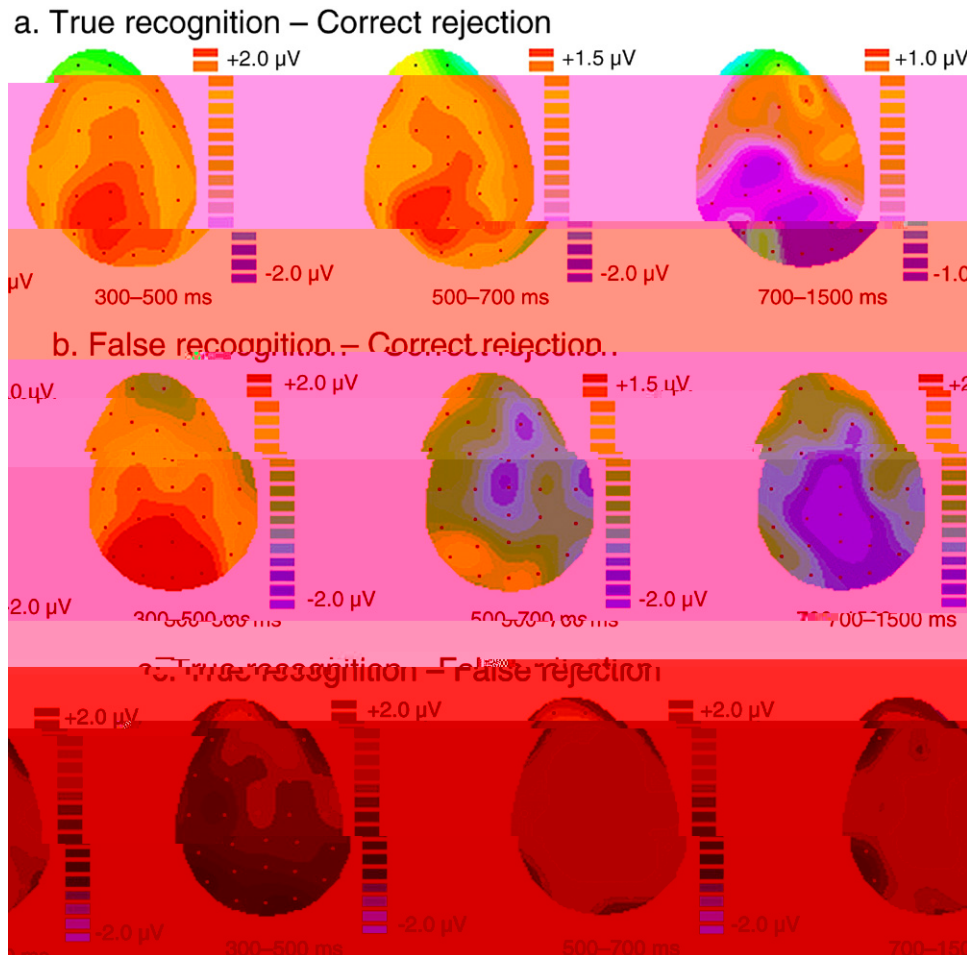


Fig. 5 – Topographic distributions of the primary ERP differences between conditions in the test phase.

clarify the interaction of the three factors (condition×location×hemisphere), the simple main effects of condition and Bonferroni post hoc analysis between conditions were computed at each level of location by hemisphere. Table 4 shows that the simple main effect of condition was significant over wide areas of the right frontal region, the middle central frontal, the middle and left central and the broad central parietal and parietal regions. The Bonferroni post hoc analysis showed that the ERP amplitudes associated with both true and false recognition were more negative than those linked to correct rejection, and true recognition was less negative than false recognition (see Table 4 and Fig. 5). The false recognition-correct rejection contrast was more widely distributed over the central, central parietal and parietal regions than the true recognition-correct rejection contrast, which was significant only over the middle parietal region. The true recognition-false recognition contrast was significant over the right frontal and middle central parietal regions. These results indicate that the late old/new effect was more widely distributed for false recognition than for true recognition and that the late slow negativity differentiated false recognition from true recognition in the right frontal and middle central parietal regions.

3. Discussion

Our study used the DRM paradigm to explore the electrophysiological mechanism underlying false recognition. The ERP method provided a moment-to-moment record of relevant neurophysiological activities at the encoding and retrieval phases to identify the roles of encoding and retrieval in eliciting false recognition of critical lures. Most previous

research has compared the ERPs differences between true recognition and false recognition only at retrieval.

3.1. Neurophysiological correlates of memory illusion at encoding

The amplitude difference of N170 between the two types of associates (classified by whether they elicited memory illusion) in the study phase should be related to semantic processing, although N170 is usually considered to index face perceptual processing (Bentin et al., 1996; Eimer, 2000). We anticipated that more active semantic processing for associates during encoding and the formation of gist representation of the study list would tend to cause the corresponding critical lure to be falsely recognized during the memory test.

In the study phase, seven associates in each word list were presented serially, the corresponding lure was activated increasingly and a gist representation was gradually established. This gist representation should influence the processing of associates at late positions of the list. One possible explanation is that, in a study list eliciting memory illusion, the semantic and associative processing of the associates at the beginning positions of the study list led to the formation of a gist representation, and the top-down processing from the

configurational processing (Itier and Taylor, 2004). It is possible that effects are observed at the N170 for this study because Chinese characters, like faces, are configurational stimuli with which the viewer has a high level of expertise (see Tanaka and Curran, 2001). By this view, more specific processing of perceptual characteristics of the items may increase the distinctiveness of studied words and enhance rejection of the lures, especially if participants were using the “distinctiveness heuristic” during retrieval (e.g., Dodson and Schacter, 2001; Hege and Dodson, 2004). Notably, this type of explanation describes the differences observed in the late serial positions in terms of what is enhanced for items not eliciting an illusion, rather than what is decreased for items eliciting an illusion. In order to make a decision on which of these patterns best exemplifies the data, comparisons across position for 859.1r2k3(of566)-423.3of567310..1(of5-376.9.1(us5673terarr.3(wo566(out.wo5603teT2(latcip3.9ult-1.444TD(((explanatturn6(for1nce)

triggering false recognitions compared with those triggering false recognitions. Urbach et al. suggested that this encoding difference associated with subsequent illusory memory (they called it “DIM”) reflects a difference in processing of item-specific information. In our current study, we included all associates in a list when comparing between ERPs for eliciting and not eliciting memory illusion. We did so because we thought that every associate in a list contributed to the establishment of a “gist” representation for the list during encoding, regardless of whether the associate was later recognized correctly or not. To compare our results with those of Urbach et al., we reanalyzed our data using their method; that is, we included only the studied words that were later recognized correctly when comparing the two conditions of eliciting vs. not eliciting memory illusion. Six of 20 participants were excluded in the reanalysis because their numbers of artifact-free trials were less than 12 for the items that were correctly recognized but did not elicit memory illusions (according to the study by Urbach et al.). ANOVA of the effects of condition \times location (frontal, central frontal, central, central parietal, parietal) \times hemisphere (right, middle, left) revealed no significant main effect of condition [$F(1,13) = 1.40, p = 0.26$] and no significant interactions between condition and other factors. Thus, we believe that the LPC difference between the two conditions (eliciting vs. not eliciting memory illusion) in our current study did not reflect any item-specific encoding difference, but rather was associated with semantic and associative processing. Similarly, Gonsalves and Paller (2000) found in a reality-monitoring paradigm that positive amplitudes of late posterior ERPs in the study phase are larger for items later falsely remembered than for those later correctly rejected, which they interpreted as the result of more vivid visual imagery. It seems that the LPC effects during encoding are not unitary, but encompass a collection of effects that can vary with the particular tasks, stimuli and strategies used.

In addition, Urbach et al. used the recall test and the single-list study-recognition procedure respectively in their two experiments. These two types of test involved more distinctive processing on item-specific information. As we know, the tendency of encoding item-specific information will increase the possibility of correct memory and reduce that of memory illusion. In this situation, the greater LPC might be related to the more encoding of item-specific information. On the contrary, an 8-list study-recognition procedure was used in our current study, participants should tend to establish a gist representation for each word list in order to retain more associates in 8 word lists. Therefore, the greater LPC for items eliciting memory illusion in our study might be related to more encoding of semantic and associative information and the formation of gist representations. This memory strategy would increase the occurrences of false recognition. This interpretation was consistent with the behavioral data. The memory illusion rate in our study was 0.63 (0.03), whereas it was 0.47 (0.06) in Experiment 2 in the study by Urbach et al. The hit rate in our study was 0.74 (0.02), whereas it was 0.91 (0.02) in the study by Urbach et al. Taken together, the different experimental procedures between the two studies led to participants' distinct memory strategies, then resulted in the opposite patterns of LPC. In summary, the LPC in encoding

phase is a complicated component, and may index diverse processes in many types of experimental tasks.

Taken together, the ERP results at encoding support the view that participants differentially encoded the semantic relations of the studied words, and that neural processes engaged at encoding predicted whether a particular word list would elicit a later memory illusion. A studied word list elicited later false recognition of the corresponding lure in the test phase, suggesting that more active processing of semantic relations established a “gist” semantic representation.

3.2. Neurophysiological correlates of memory illusion at retrieval

We found that ERPs were more negative for correctly rejected new words than for true and false recognition starting around 300 ms after the test word presentation. The ERP waveforms for true and false recognition revealed equal early N400 (300–500 ms) ERP old/new effects (new > lure = studied), having a central parietal maximum. N400 varies systematically with the processing of semantic information, and its amplitude varies with semantic relationships between individual words in lists, when the words are attended (Bentin et al., 1995; Brown and Hagoort, 1993; Kutas and Federmeier, 2000). Düzel et al. (1997) also observed an N400 old/new effect in the DRM paradigm when both the study and test modalities were visual.

Several recent studies have identified a frontally distributed N400-like old/new effect, which was termed by Curran (1999, 2000) the “FN400”. This effect has been hypothesized to be related to familiarity because FN400 discriminates between true recognition and correctly rejected new words, but not between true and false recognition (Curran and Friedman, 2004; Nessler and Mecklinger, 2003). This pattern has been observed when similar lures are plurality-reversed words (Curran, 2000), semantically similar words (Nessler et al., 2001) and mirror-reversed pictures (Curran and Cleary, 2003). Rugg et al. (1998b) discriminated two kinds of old/new effects in a similar time window (300–500 ms), which have different scalp distributions: a parietal old/new effect and a frontal old/new effect. Given that the parietal old/new effect was similar in size for recognized and unrecognized old words and insensitive to depth of processing, Rugg et al. identified the effect as a neural correlate of implicit memory. They suggested that the frontal old/new effect reflects item “familiarity” because it was found for recognized old words but not for unrecognized old words and because it was insensitive to the depth of study processing. We found that the old/new effect between 300 and 500 ms was focused at parietal sites, which may be correlated with semantic priming. According to the aforementioned view on the role of encoding in eliciting later false recognition, the more active processing of semantic relations between items in a word list establishes a “gist” semantic representation, which increases the possibility of the occurrence of false recognition. Thus, the equal N400 old/new effects for true and false recognition should reflect similar semantic priming. Future studies will need to systematically and deeply explore the differences between the N400 and FN400 old/new effects.

The parietal ERP (500–700 ms) was more positive for true recognition than for false recognition and correct rejection

(studied > lure = new), and for smaller parietal old/new ERP effects for false than for true recognition, suggesting less active recollection. Together with the typical left-lateralized distribution of true recognition-correct rejection contrast, these results complement other studies showing a relationship between the parietal old/new effect and recollection. The parietal old/new effect is related to the recollection of specific information or associative information, source recollection and discrimination between studied words and nonstudied conjunctions (Allan et al., 1998; Donaldson and Rugg, 1998, 1999; Rubin et al., 1999; Wilding and Rugg, 1996). Furthermore, the parietal old/new effect is larger when participants judge recognized items as “remembered” than “known” (Düzel et al., 1997; Rugg et al., 1998a), and larger for words studied under deep than under shallow-encoding conditions (Rugg et al., 1998b). Assuming recollection is more prevalent for the hits than for false alarms (Yonelinas, 2001), these results are consistent with the hypothesized association between recollection and the parietal old/new effect.

The parietal and frontal electrodes (especially at F4) identified a late negative slow wave that differentiated false recognition from true recognition and correct rejection of new words in the late time window (700–1500 ms). This late slow negativity was greater for false recognition than for true recognition and correct rejection. Nessler and Mecklinger (2003) and Nessler et al. (2001) found a similar late posterior negativity (LPN) elicited by false recognition, which they localized to the anterior cingulate cortex (ACC) activity by dipole analysis. Nessler et al. thought that the ACC activation might reflect the attentional modulation of an enhanced response conflict. This conflict might be caused by old responses to familiar lures in the presence of little or no conscious recollection of item-specific information. In other words, participants should be more confident when they respond “yes” to studied words and “no” to new words than when responding “yes” to lures, because of the recollection of more perceptual details for studied words and the semantic anomaly of new words. The presence of the lures enhances response conflicts and, by this, strengthens the need for active monitoring processes. Johansson and Mecklinger (2003) suggested that the LPN comprises at least two functionally distinct components: one associated with action monitoring in tasks characterized by high levels of response conflict (as in the present study), and the other with processes related to the retrieval of attribute conjunctions.

In our study, late ERP differences also occurred at the frontal sites (significant at F4). A number of functional imaging studies have debated the possible contribution on the right frontal sites to functions involved in strategic retrieval effort and post-retrieval evaluation processes (Allan et al., 1998; Curran et al., 2001; Schacter, 1996; Wilding, 1999). In their PET study, Schacter et al. (1996a) distinguished between two brain regions involved in the mental effort associated with searching memory and the actual recollection of previously studied information. They found that increased blood flow in the hippocampus formation during episodic memory retrieval was associated with the conscious recollection of studied word, whereas the right anterior prefrontal cortex may play an important role in efforts to retrieve target words. Recent electrophysiological evidence also supports the idea that the

right frontal differences reflect post-retrieval evaluation processes. For example, in their ERP study, Curran et al. (2001) found that good performers showed better discrimination between old words and lures, suggesting that they were more likely to carefully evaluate activated information or attempt additional retrieval before making a response. Although the neural sources of scalp-recorded ERPs cannot be localized precisely, the effect in the right frontal electrodes supposedly reflects the involvement of the right prefrontal cortex in episodic retrieval tasks (Mecklinger, 2000; Nessler et al., 2001). A similar interpretation was offered to explain right prefrontal activation obtained in an event-related fMRI study using the “remember-know” paradigm (Henson et al., 1999). Right frontal activity associated with “know” judgments was greater for old than for new words, but such differences were absent for “remember” judgments. Henson et al. suggested that frontal monitoring processes might be required for choosing to respond “know” or “new” to a familiar word, but might not be necessary when the spatiotemporal context of the study episode is clearly “remembered”.

Fig. 4 and Table 4 suggest that the late slow wave was more negative for false recognition than for true recognition, whereas there was no difference between true recognition and correct rejection at the right frontal site (F4). We interpret this to reflect different levels of effort in the post-retrieval evaluation processes. The strong feeling of familiarity and the absence of retrieval of perceptual details made it more difficult to respond “yes” to critical lures than to studied words. Specifically, the right frontal old/new effect was negative for false recognition in our present study, whereas the effect was usually reversed in polarity in most other studies (see Johansson and Mecklinger, 2003, for a review). The available data do not permit us to give a specific interpretation about this difference between our study and other studies. There is no consensus on the precise functional significance of the late and long-lasting right frontal old/new effect. Given the difficulty in interpreting the relationship between the right frontal effect and LPN by their opposite polarities and overlapping temporal distribution reported in other studies, we propose that the similar polarities and timing characteristics between the right frontal effect and the LPN exhibited in our current study reflect a close temporal and functional relationship between these neural activities. The broad temporal extension may reflect a continued post-retrieval evaluation or rechecking of the validity of the memory decision.

The parietal and frontal distributions of the late negativity may reflect the interaction of two local generators. Gehring and Knight (2000) found that activity in the medial frontal cortex, most likely in the ACC, is associated with action monitoring (detecting errors and behavioral conflict) and depends on activity in the lateral prefrontal cortex. They also suggested that the lateral prefrontal cortex seemed to interact with the ACC in monitoring behavior and in guiding compensatory systems. Most models of executive control consistently suggest that the PFC exerts a top-down influence on early and higher sensory areas to maintain goal-oriented behavior in different task environments. Regardless of the underlying mechanism, clarifying the precise nature of the interaction between the right frontal slow wave and the LPN in

memory retrieval tasks remains a significant objective for further research.

In conclusion, we explored the roles of encoding and retrieval in eliciting memory illusion. We observed two differences in study-phase ERPs between two types of associates classified by whether they elicited or did not elicit memory illusion. These findings indicate that neural processes engaged by the encoding process predict whether a corresponding critical lure would be falsely recognized later. We recorded the ERPs that varied with later memory performance while participants memorized visually presented associates. The smaller occipital N170 and larger LPC amplitudes for associates eliciting later memory illusion can be interpreted as more active semantic-associative processing or as a gist representation established for those items. This interpretation is supported by the serial-position analysis of the ERPs at encoding. Three ERP components were identified at retrieval. The equal early (300–500 ms) central parietal old/new effects for true and false recognition reflected similar semantic priming. The parietal ERP (500–700 ms) old/new effect was greater for true than for false recognition, reflecting the recollection processes. A late slow negativity (700–1500 ms) distributed in the parietal and right frontal electrode sites differentiated between true recognition and false recognition. These data may reflect the interaction between the right frontal slow wave and the LPN in action monitoring and post-retrieval evaluation. Our data also confirmed that both encoding and retrieval are involved in eliciting false memory in the DRM paradigm. These data are consistent with the activating-monitoring framework developed by [Roediger et al. \(2001\)](#), which assumes that studied items activate related lures during the study episode, and that false recognition results from a failure to correctly monitor the source of this activation. From this perspective, it seems reasonable that both encoding and retrieval play an important role in the generation of false memory in the DRM paradigm. The parietal and frontal distributions of LPC at encoding and the late negativity at retrieval may imply a

break of 3–5 min between each study-test cycle. Including the electrode application and removal, the experiment lasted about 3 h.

4.4. ERP recording

The electroencephalogram (EEG) was recorded from 32 scalp electrodes mounted on an elastic cap according to the extended 10–20 System (FP1, F7, F3, FZ, FT7, FC3, FCZ, T7, C3, CZ, TP7, CP3, CPZ, P7, P3, PZ, O1, OZ and the corresponding right hemisphere sites). The skin resistance of each electrode was <5 k Ω . The right mastoid was recorded as an additional channel. All scalp electrodes were referenced to the left mastoid and were re-referenced offline to both mastoids. Eye blinks and vertical eye movement were monitored with electrodes located below the right eye. The horizontal electro-oculogram was recorded from electrodes placed 1.5 cm lateral to the left and right external canthi. The EEG was amplified (band pass 0.15–40 Hz) and digitized at a sampling rate of 250 Hz. The ERPs in each stimulus condition were averaged separately off-line with averaging epochs beginning 200 ms before the stimulus onset and continuing for 1700 ms. Trials contaminated by eye blinks, eye movements or muscle potentials, as indicated by voltages in excess of $\pm 50 \mu\text{V}$ at VEOG, HEOG, FP1 or FP2, were excluded.

4.5. Data analysis

4.5.1. Behavioral data

Reaction time was defined as the interval between the appearance of the test item and the participant's keypress. Data were averaged separately for each response condition.

4.5.2. ERP data

The ERPs recorded during the study phase were computed according to whether the corresponding lure was or was not recognized later. Participants' responses to associates in the study phase were classified as "eliciting memory illusion" if participants later incorrectly recognized their corresponding critical lures, or "not eliciting memory illusion" if participants later correctly rejected their corresponding critical lures. The serial-position analysis was performed to test the gist representation hypothesis. Each studied list was composed of seven associates that were always presented in a constant serial order in the study phase. To ensure that there were enough trials to provide overlap of the EEG in each condition, two parts were defined from the original seven positions in each study list in the serial-position analyses. The early part included the first three serial positions (positions 1, 2 and 3), and the late part included the last three serial positions (positions 5, 6 and 7). The ERPs for associates were averaged within each part.

The ERPs recorded during the test phase were selectively averaged for the following conditions: old items given old responses (true recognition), lure items given old responses (false recognition) and new items given new responses (correct rejection). Because there were too few new responses to lure words and to old words, and too few old responses to new words (less than 16 good trials), these conditions were excluded from further analysis.

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Appendix A

The pool of Chinese associative word lists was created using procedures similar to those of Deese (1959) and Roediger and McDermott (1995). We generated 233 Chinese two-character words, which were either nouns or adjectives. These 233 words were used as critical items (lure words). Eighty graduate and undergraduate students from Peking University (18–25 years old) were asked to write as many associates as possible for each given critical item in a word generation test, and the 15 words generated most frequently were used to compose the associative list of a critical item. Another 80 graduate and undergraduate students from Peking University were recruited to arrange the associates in each list according to the degree of their semantic relationships to the critical item in a word-rating test, and the mean order of every associate within each list was calculated. Finally, words within a list were arranged in order of decreasing relatedness to the critical item, as described by Roediger and McDermott (1995). Because this pool was the only standard Chinese version, all relevant studies conducted in China selected materials from this pool.

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