Distinct Patterns of Neural Activity during Memory Formation of Nonwords versus Words

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Abstract

■ Research into the neural underpinnings of memory formation has focused on the encoding of familiar verbal information. Here, we address how the brain supports the encoding of novel information that does not have meaning. Electrical brain activity was recorded from the scalps of healthy young adults while they performed an incidental encoding task (syllable judgments) on separate series of words and "nonwords" (nonsense letter strings that are orthographically legal and pronounceable). Memory for the items was then probed with a recognition memory test. For words as well as nonwords, event-related potentials differed depending on whether an item would subsequently be remembered or forgotten. However, the polarity and timing of the effect varied across item type. For words, subsequently remembered items showed the usually observed positive-going, frontally distributed modulation from around 600 msec after word onset. For nonwords, by contrast, a negative-going, spatially widespread modulation predicted encoding success from 1000 msec onward. Nonwords also showed a modulation shortly after item onset. These findings imply that the brain supports the encoding of familiar and unfamiliar letter strings in qualitatively different ways, including the engagement of distinct neural activity at different points in time. The processing of semantic attributes plays an important role in the encoding of words and the associated positive frontal modulation. ■

INTRODUCTION

The ability to encode new experiences into long-term memory is essential for both humans and nonhumans as it enables the organism to learn. Since the late 1970s, insights have been gained into the brain mechanisms that underlie memory formation (for reviews, see Paller & Wagner, 2002; Friedman & Johnson, 2000; Wagner, Koutstaal, & Schacter, 1999; Rugg, 1995). Most studies have used words as stimulus material, focusing on the question of how the brain supports the encoding of familiar verbal information. Relatively little is therefore currently known about how the brain supports the encoding of other kinds of material, such as information that is novel, devoid of meaning, or nonverbal. Here, we address this issue by contrasting the encoding of words and "nonwords," unfamiliar letter strings that are orthographically legal and pronounceable, but which do not carry meaning. Scalp-recorded electrical brain activity is used to determine both temporal and qualitative aspects of nonword learning.

Sanquist, Rohrbaugh, Syndulko, and Lindsley (1980) popularized the "subsequent memory" approach to study memory formation. This procedure uses a backsorting method to identify neural activity that predicts whether an event will later be remembered or forgotten. Neural activity is recorded while volunteers study a number of items, after which memory for the items is tested. Activity that differs as a function of subsequent memory performance ("subsequent memory effects") is considered to play a role in successful encoding.

Early subsequent memory research focused on the encoding of verbal material and, until the late 1990s, primarily examined event-related potentials or ERPs (small, event-locked changes in the brain's electrical activity). It has consistently been found that words that are subsequently remembered are, at study, associated with a more positive-going waveform than words that are subsequently forgotten (Paller & Wagner, 2002; Friedman & Johnson, 2000; Rugg, 1995). This effect tends to be maximal over frontal scalp sites, typically starts around 500 msec, and can persist for 1 or 2 sec. In light of evidence that the effect is larger in tasks that require "deep" as opposed to "shallow" processing (Guo, Zhu, Ding, Fan, & Paller, 2004; Otten & Rugg, 2001a, 2001b; Friedman, Ritter, & Snodgrass, 1996; Paller & Kutas, 1992; Paller, Kutas, & Mayes, 1987; Sanquist et al., 1980), larger in semantic association tasks (Weyerts, Tendolkar, Smid, & Heinze, 1997), and in intentional memorization tasks more pronounced when subjects use elaborative as opposed to rote rehearsal strategies (Fabiani, Karis, & Donchin, 1990; Karis, Fabiani, & Donchin, 1984), it has been suggested that the effect reflects the extent to which a word's higher-level attributes (such as semantic, phonological, and/or associative features) are processed. The more an item is elaborated on at study, the more likely it is that the item is

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turned into a durable representation that can be accessed again at a later time (cf. Craik & Lockhart, 1972).

In support of the idea that higher-level attributes play a crucial role in the encoding of familiar verbal information, functional magnetic resonance imaging (fMRI) studies have more recently found that activity in a number of brain regions, including the left prefrontal cortex, differs between words that are subsequently remembered versus forgotten (Wagner, Schacter, et al., 1998; see Paller & Wagner, 2002 for review). The left prefrontal cortex has, in the language literature, been implicated in semantic (ventral inferior frontal gyrus) and phonological (dorsal inferior frontal gyrus) processing (Poldrack et al., 1999). In addition, the left prefrontal cortex plays a role in semantic working memory (Gabrieli, Poldrack, & Desmond, 1998). As argued for ERP subsequent memory effects, it has therefore been suggested that effects in this part of the cortex reflect the degree to which semantic and phonological features are elaborated on at study (Buckner, Logan, Donaldson, & Wheeler, 2000; Wagner et al., 1999; Buckner & Koutstaal, 1998; Wagner, Schacter, et al., 1998). The output of such processing is then relayed to the medial-temporal lobe, where it is processed further into a cohesive memory trace. Although inferring the intracerebral origins of scalp-recorded activity is difficult, a link has been drawn between activity in the left prefrontal cortex and the positive frontal ERP modulation associated with successful encoding (Friedman & Johnson, 2000).

The apparent importance of the processing of higher-level attributes in memory formation begs the question how memory encoding operates on items that have few or no semantic attributes, and in situations that do not involve semantic processing. Early on it was realized that there is not a single pattern of neural activity that explains effective encoding in all circumstances. Although a positive frontal subsequent memory effect occurred in the majority of ERP studies, a more posteriorly distributed effect has been observed during the encoding of distinctive words via rote rehearsal (e.g., Fabiani et al., 1990; see Rugg, 1995, for review). In addition, brain regions other than the prefrontal cortex are sensitive to subsequent memory performance (Paller & Wagner, 2002).

Several studies have investigated whether type of study task and type of study material affect neural correlates of encoding. These studies have revealed qualitatively different subsequent memory effects for words encoded in nonsemantic (e.g., syllable or orthographic) as opposed to semantic study tasks (Otten, Henson, & Rugg, 2002; Davachi, Maril, & Wagner, 2001; Otten & Rugg, 2001a). Similarly, the encoding of nonverbal rather than verbal material has been shown to involve distinct brain regions, including a relatively greater involvement of the right hemisphere (Kirchhoff, Wagner, Maril, & Stern, 2000; McDermott, Buckner, Petersen, Kelley, & Sanders, 1999; Kelley et al., 1998; Wagner, Poldrack, et al., 1998). Finally, different kinds of verbal material, such as low- versus high-frequency words, have also been associated with different patterns of encoding-related activity (Guo et al., 2004; Chee, Westphal, Goh, Graham, & Song, 2003). Together, these findings suggest that memory formation is supported by different brain mechanisms depending on both the content of the to-be-remembered information and the type of processing engaged while that information is encountered (cf. Paller & Wagner, 2002; Wagner et al., 1999).

Past studies, however, have focused on the encoding of material that is familiar and whose encoding can therefore rely on the reactivation of preexisting neural and cognitive representations, including higher-level semantic and associative features. But how are items without preexisting representations transformed into a durable representation? Although we are able to learn new information, such as a foreign language, the neural processes supporting novel item learning are mostly unknown. The primary question in the present experiment was how items that have not been encountered previously, and therefore do not yet have meaning, are encoded into long-term memory.

The general issue of novelty has received a great deal of attention in the neuroimaging and animal literature (see Nyberg, 2005; Knight & Nakada, 1998 for reviews). These studies have identified a number of brain regions, especially in the prefrontal and medial-temporal cortex, that are associated with novelty processing. However, these studies have not defined novelty in the same way as intended here. As pointed out by Martin, Wiggs, and Weisberg (1997), among others, ''novelty'' can be defined in a number of ways, including inherent characteristics of an item and the level of experience with items and tasks. Most neuroimaging studies have defined novelty in terms of the initial versus repeated occurrence of material that is known (e.g., repeated words or pictures), the unusual appearance of a familiar item (e.g., a word in a different font or color), or the appearance of an item in an unusual context (e.g., an emotionally charged word in a series of neutral words). Thus, these studies have little bearing on the question of how items without preexisting representations are encoded into memory.

Two previous studies have contrasted the encoding of familiar and unfamiliar, meaningless stimuli. Van Petten and Senkfor (1996) compared ERP subsequent memory effects for words and novel visual patterns. Whereas a positive, frontally distributed effect was observed for words, no reliable effect emerged for novel patterns. These findings are difficult to interpret, however, as type of study material (words vs. visual patterns) was confounded with type of study task (semantic vs. nonsemantic judgment).

Clark and Wagner (2003) used a subsequent memory paradigm to investigate the role of phonological processing in novel item learning. fMRI signals were acquired while subjects made syllable judgments about English words, pseudo-English words (nonsense letter strings

derived from English words), and foreign words. Activity in the left dorsal inferior frontal gyrus (an area specialized in phonological analysis; Poldrack et al., 1999) was found to predict whether an item would subsequently be remembered or forgotten. This effect was present for words and pseudowords, but was larger for pseudowords. Clark and Wagner, therefore, concluded that the encoding of novel letter strings into long-term memory involves phonological control processes. This may be premature, however, as it could be argued that pseudowords that are derived from words (by one letter in the case of Clark & Wagner, 2003) can be remembered, at least in part, because subjects recognize and activate the underlying word (Deacon, Dynowska, Ritter, & Grose-Fifer, 2004). It is therefore necessary to assess subsequent memory effects for nonderived letter strings, such as foreign words. Unfortunately, the experiment was not designed to enable enough foreign words to be remembered.

Here, we took advantage of a stimulus set that was originally developed to address the functional significance of the N400 (see Kutas & Federmeider, 2000, for a description of this ERP component). Deacon et al. (2004, Experiment 2) created letter strings that are pronounceable and orthographically legal according to the rules of the English language, but which do not correspond to actual English words. Crucially, unlike most ''nonwords'' used in the memory and language literature (including Clark & Wagner, 2003, described above), the strings were not derived from existing words. Thus, the processing of these nonwords cannot be based on a partial or complete activation of properties of the underlying word. A control experiment confirmed that these stimuli, indeed, do not easily trigger words (Deacon et al., 2004). These nonderived nonwords are well suited to study novel item learning. Although composed of famil-

iar elements (letters and sounds), their configuration is novel and without meaning. Yet, their similarity to words in all other respects allows an assessment of the influence of semantic attributes on memory encoding in relative isolation, and a comparison with a stimulus class that has been the focus of previous studies.

Electrical brain activity was recorded from the scalps of healthy young adults while they performed an incidental encoding task (syllable judgments) on the above nonderived nonwords and words. After a delay, memory for the items was tested with a recognition task. The primary question of interest was whether neural activity predictive of later memory performance differs between nonwords and words. This was examined by considering the timing, amplitude, and scalp distribution of subsequent memory effects in each stimulus class. To get around the inherent problem that memory is poorer for novel than familiar material, nonwords were assessed with a shorter list length (102 vs. 150 critical study items) and a shorter study–test delay (5 vs. 30 min) than words (see Figure 1). This ensured that enough nonwords would be remembered yet enough words forgotten, allowing the computation of subsequent memory effects for both item types. Similar manipulations have been used for comparisons across groups that differ in memory performance (e.g., young vs. elderly individuals; Morcom, Good, Frackowiak, & Rugg, 2003), and in a previous study of novel item learning (Van Petten & Senkfor, 1996). Importantly, these manipulations do not compromise the ability to evaluate effects of novelty on memory encoding. The positive frontal subsequent memory ERP effect typically elicited by words has been found despite variations in number of experimental items (from tens to a few hundred; compare, e.g., Fernández et al., 1998; Fabiani et al., 1990; Sanquist

Figure 1. Experimental design. (A) Trial structure of experimental tasks. During the study and test phases, volunteers viewed a number of words or nonsense letter strings (''nonwords''), presented one at a time. Each item was preceded by a neutral warning stimulus. (B) Experimental procedure. During the study phase, volunteers performed an incidental encoding task (syllable judgments) on separate series of words and nonwords. The task on words was always performed first. Memory for all items was then tested with surprise recognition memory tests. The first task always comprised a memory test for the nonwords, and the second for the words. The reverse presentation order of words and nonwords during the study and test phases allowed the differential study–test delay needed to balance memory performance for words and nonwords.
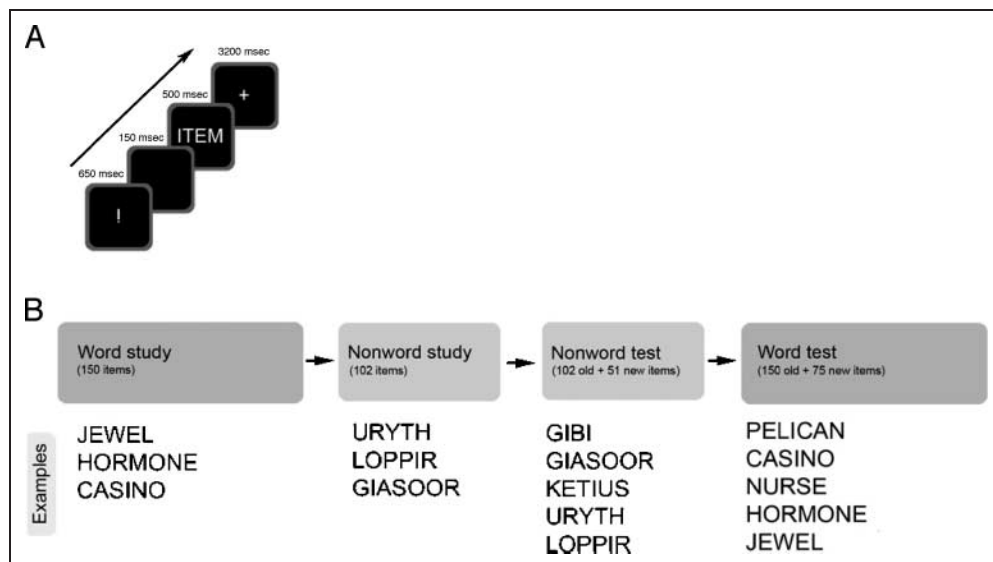
et al., 1980 with Weyerts et al., 1997; Van Petten & Senkfor, 1996; Paller et al., 1987) and study–test delay (from a few minutes to 45 min; compare, e.g., Sommer, Schweinberger, & Matt, 1991; Fabiani et al., 1990; Sanquist et al., 1980 with Otten, Quayle, Akram, Ditewig, & Rugg, 2006; Otten & Rugg, 2001b). Thus, small differences in list length and study–test delay are, by themselves, not sufficient to alter this effect.

In addition to novel item learning, the above design enabled an evaluation of the functional significance of ERP subsequent memory effects. As mentioned earlier, it is currently unknown whether the frontally distributed positive ERP deflection usually associated with subsequently remembered items reflects the additional processing of semantic attributes, phonological attributes, or both (Paller & Wagner, 2002; Friedman & Johnson, 2000; Wagner et al., 1999; Rugg, 1995; Paller et al., 1987). By manipulating the presence of semantic attributes in a phonological processing task, it becomes possible to shed light on the particular attribute(s) that underlies the effect. If syllable judgments on words elicit a frontally distributed positive subsequent memory effect, the effect may either reflect the processing of phonological attributes or the incidental processing of semantic attributes. Crucially, if the same effect is observed for syllable judgments on letter strings that do not carry meaning (i.e., nonderived nonwords), the effect can only reflect the processing of phonological attributes. If, on the other hand, no frontal positivity is observed for nonwords, the effect most likely reflects the processing of semantic attributes.

METHODS

Participants

The experimental procedures were approved by the University College London and University College London Hospitals joint ethics committee. Written informed consent was obtained from 22 native English-speaking volunteers who were paid to participate in the experiment. All volunteers reported to be right-handed, healthy without neurological and psychiatric histories, and to have normal or corrected-to-normal vision. The analyses presented here are based on 18 volunteers (age range 19–25 years, 15 women). The data from two volunteers were excluded because of uncorrectable eye movements, and a further two did not forget a sufficient number (i.e., at least 15) of words.

Stimulus Lists

The stimulus lists were constructed from a pool of 499 words and a pool of 238 nonsense letter strings (nonwords). All items were between four and seven letters in length. The words were taken from Kučera and Francis (1967) and had a written frequency of 1–30 occurrences per million. Three sets of 75 words each were selected at random from the word pool with the constraint that the sets had the same distributions of word lengths and the same distributions of items with odd and even number of syllables. Two of these sets were used to create a study list of 150 items, with the remaining set added to create a test list of 225 items. The sets were rotated across subjects to form different study–test list combinations so that, across subjects, each item could appear as either old or new. The words were allocated to the study and test lists in a pseudorandom order (restriction that no more than five successive items were of the same experimental condition) and each list was divided into three blocks of equal length. Short rest breaks were given between blocks. Two filler words were added to the beginning of each block. A further 15 words were selected from the word pool to create practice lists.

The nonwords were taken from Deacon et al. (2004, Experiment 2). As explained in the Introduction, the nonsense letter strings were orthographically legal and pronounceable but not derived from English words. Three sets of 51 nonwords each were selected pseudorandomly from the nonword pool to form a study list of 102, and a test list of 153, items. As for the words, the sets were equated with respect to item length and number of syllables, and rotated across subjects. The lists were ordered pseudorandomly and split into two blocks of equal length with two filler items added to each block. Fifteen further nonwords were used to create practice lists. For both word and nonword lists, the ratio of items with an even versus odd number of syllables was 2:1 to accommodate the fact that most nonwords had an even number of syllables.

Tasks and Protocol

The experiment consisted of an incidental study phase, followed by a surprise recognition memory test. Following electrode application (see the EEG Acquisition section), volunteers were seated in front of a computer monitor and shown series of words and nonwords. Because of the need to balance memory performance across stimulus categories, words and nonwords were presented in separate blocks with a fixed presentation order and different list lengths. Figure 1 illustrates the design. Each volunteer always initially saw a series of 150 critical words, followed by a series of 102 critical nonwords. These two series comprised the study phase. During this phase, volunteers were asked to silently count the number of syllables in each letter string and decide whether this number is odd or even. One of two response buttons had to be pressed according to each decision. Both speed and accuracy were stressed. Responses were given via a response box on a table in front of the volunteer with the index and middle fingers of the right hand (responding finger counterbalanced across subjects). Short practice lists were given prior to the word and nonword

blocks to familiarize volunteers with the task. Total duration of the study phase was approximately 30 min.

Immediately upon completion of the study phase, volunteers received separate recognition memory tests for the nonwords and words. The tests incorporated the remember–know procedure to separate responses based on recollection versus a general feeling of familiarity (Tulving, 1985). Volunteers were not informed that their memory would be tested until this point in the experiment. To balance memory performance, the tests for words and nonwords were again given in separate blocks and with a fixed presentation order. The test for nonwords was always presented first. Accordingly, each volunteer initially saw a series of 153 critical nonwords (102 old, 51 new), followed by a series of 225 critical words (150 old, 75 new). The reverse presentation order of words and nonwords in the study versus test phases (i.e., nonwords were presented last in the study phase but first in the test phase) accomplished the intended variable study–test delay to balance memory performance. For nonwords, the time between the end of the study list and start of the test list was approximately 5 min. For words, the delay was 30 min.

In each memory test, all previously studied items were presented again, along with items not experienced before in the experiment. Volunteers were asked to make a "new," "remember," or "know" judgment about each item. A "new" judgment was required if they did not recognize the item from the study phase, a "remember" response when they both recognized the item and remembered something specific about its initial encounter, and a "know" response when they recognized the item but only had a general feeling that the item was familiar. One of three buttons had to be pressed with the right index, middle, and third fingers according to each decision (responding finger counterbalanced across subjects). Both speed and accuracy were stressed. Short practice lists were given before the nonword and word tests to familiarize volunteers with the task. The test phase lasted approximately 45 min, after which volunteers were debriefed and paid for their time.

All letter strings were shown one at a time in central vision in white uppercase letters (Helvetica font) on a black background. Stimulus duration was 500 msec with an interval of 4.5 sec in between stimulus onsets. Eight hundred milliseconds before the onset of each item, a neutral warning stimulus (an exclamation mark) was presented for 650 msec, followed by a 150-msec blank period. A fixation point (a plus sign) was continuously present on the screen other than when stimuli were presented. Letter strings subtended approximate visual angles of 0.7° vertically and 1.3–2.6° horizontally.

EEG Acquisition and Analysis

Electroencephalogram (EEG) was recorded from 31 scalp sites using silver/silver–chloride electrodes embedded in an elasticated cap (montage 10; www.easycap.de/easycap/e/electrodes/13_M10.htm). Vertical and horizontal eye movements were recorded bipolarly from electrodes placed above and below the right eye and on the outer canthus of each eye. All signals were amplified, band-pass filtered between 0.01 and 100 Hz (3 dB roll-off), and acquired continuously at a rate of 500 Hz (12-bit resolution).

Signals were digitally filtered to remove frequencies above 20 Hz (96 dB roll-off, zero phase shift filter), and then downsampled to 125 Hz. EEG epochs extending from 100 msec before item onset until 1948 msec thereafter were extracted from the continuous record. ERP waveforms were created for each electrode site and stimulus category by averaging epochs separately for study items subsequently given a "remember," "know," or "new" judgment. Waveforms were aligned to the 100-msec prestimulus baseline. Blink artifacts were minimized by estimating and correcting their contribution to the ERP waveforms via a standard regression technique (Rugg, Mark, Gilchrist, & Roberts, 1997). Trials on which horizontal or nonblink vertical movements occurred were excluded from the averaging process, as were trials containing EEG drifts ($\pm50~\mu V$) or A/D saturation. Trials with incorrect study judgments, no response, or a response faster than 200 msec were also excluded from analysis. Waveforms were based on a minimum of 15 artifact-free trials and reconstructed to represent recordings with respect to linked mastoids. Collapsed across "remember" and "know" responses (see Results), the waveforms for remembered and forgotten items were based on a mean of 93 and 37 trials for words, and 47 and 33 trials for nonwords.

RESULTS

Task Performance

Study

Judging the number of syllables in a word took, on average, 1094 msec ($SD = 369$ msec) and was correct on 96% ($SD = 4\%$) of trials. Judgments about nonwords took 1314 msec ($SD = 372$ msec) with an accuracy of 86% ($SD = 8\%$). Response times were longer, and accuracy lower, for nonwords [paired-samples $t(17) = 5.27$ and -8.30, respectively, both $p < .001$].

To assess whether study RTs differed depending on whether an item was successfully encoded into memory, the time to respond to an item was compared depending on the kind of judgment given to the item in the later recognition test. Mimicking the way in which the EEG data were analyzed (see below), response times were contrasted between items that were subsequently remembered (received a "remember" or "know" judgment) versus forgotten (received a "new" judgment). Response times for these items did not differ reliably. This was true for both words [1092 vs. 1101 for remembered and

Figure 2. Neural activity predictive of memory formation for words. Group-averaged ERP waveforms elicited at study by words that were remembered versus forgotten in the subsequent recognition memory test. Waveforms are shown for all 29 scalp sites (montage 10; www.easycap.de/easycap/e/electrodes/13_M10.htm). Positive values are plotted upward.
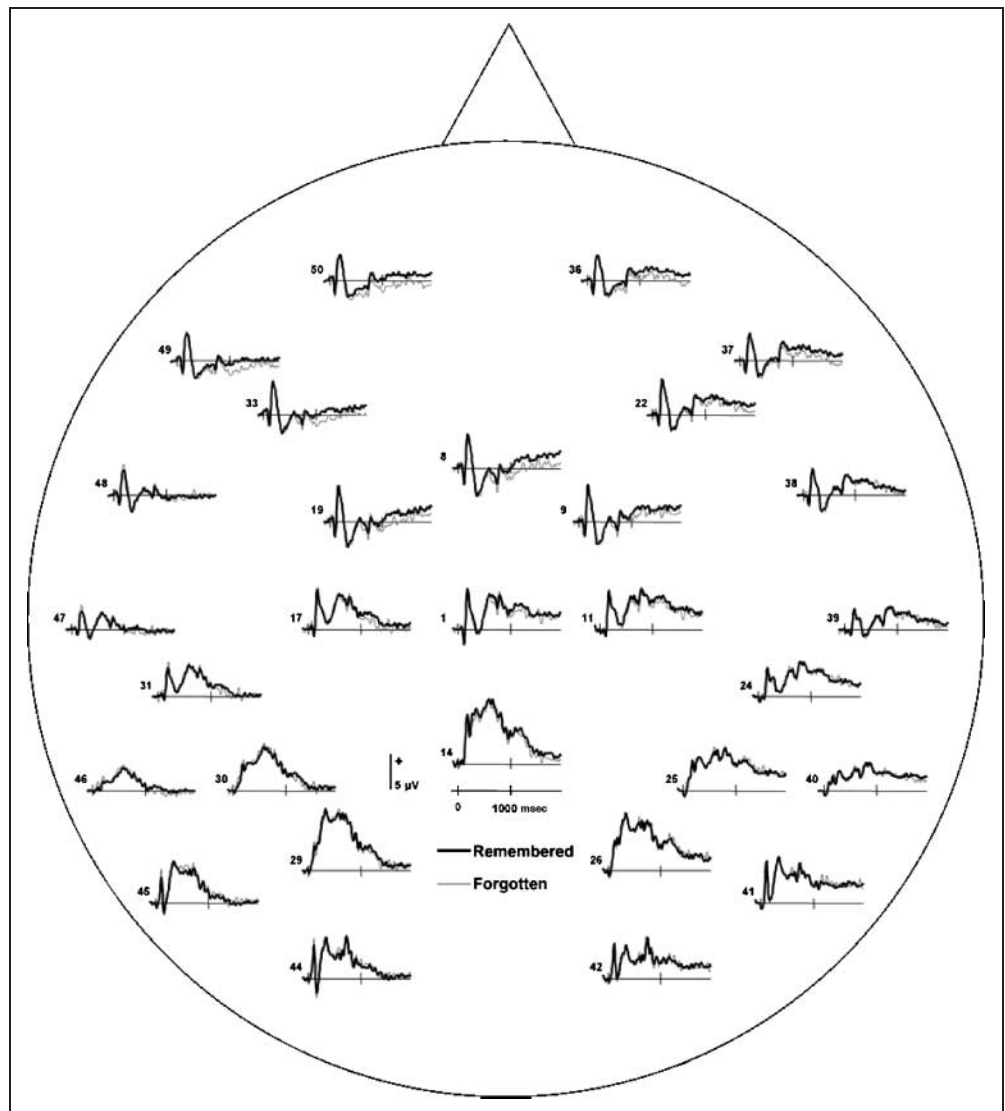
forgotten items, respectively; $t(17) = 0.59$, *ns*] and nonwords [1307 vs. 1330 msec; $t(17) = 1.07$, *ns*].

Test

Memory performance is shown in Table 1. Recognition accuracy was assessed with the discrimination measure $p(\text{Hit}) - p(\text{False Alarm})$ (Snodgrass & Corwin, 1988), separately for "remember" and "know" responses. To provide an index of familiarity, "know" responses were mathematically adjusted for being constrained by "remember" responses, using the assumption of independence (Yonelinas & Jacoby, 1995). Accordingly, the probability that a decision was based on a sense of familiarity was estimated as $p(\text{Know})/(1 - p(\text{Remember}))$. This formula was applied to both hits and false alarms.

Collapsed across recollection and familiarity, recognition accuracy was 0.61 for words and 0.39 for nonwords. The higher accuracy for words was due to an increase in both recollection [0.30 vs. 0.17; $t(17) = 6.18, p < .001$]

and familiarity [0.31 vs. 0.22; $t(17) = 2.30, p = .034$]. Importantly, there was no reliable interaction between stimulus category and memory type [$F(1, 17) = 1.40$,

Table 1. Recognition Memory Performance

| Item Type | Recognition Judgment | | |
	Remember	Know	New
Proportion of Responses			
Old			
Word	0.35 (0.12)	0.37 (0.13)	0.28 (0.06)
Nonword	0.21 (0.10)	0.36 (0.09)	0.42 (0.10)
New			
Word	0.04 (0.04)	0.22 (0.11)	0.73 (0.14)
Nonword	0.05 (0.05)	0.23 (0.09)	0.72 (0.11)

Values are across-subject means (*SD*), $n = 18$.

p = .25]. Thus, although memory performance was better for words on the whole, recollection and familiarity contributed equally to the recognition of nonwords and words.

EEG Data

Subsequent Memory Effects

For the EEG data, the primary interest was in ERP waveforms elicited by study items, distinguished by performance in the later recognition test (i.e., subsequent memory effects). Because only a subset of subjects gave sufficient numbers of "remember" as well as "know" judgments to compute separate ERPs for these two response categories, the recognition memory test was treated as a conventional old/new decision task. Accordingly, study items were classified as "remembered" when they received either a "remember" or "know" judgment, and as "forgotten" when they were misclassified as "new."

The group-averaged ERP waveforms for words and nonwords that were later remembered versus forgotten are shown in Figures 2 and 3, respectively. As can be seen, the ERPs elicited by words differ from around 600 msec onward, an effect that takes the form of a more positive-going waveform for subsequently remembered than subsequently forgotten words. The difference is largest over frontal electrode sites and persists throughout the epoch, although it is small before about 1 sec. The ERPs elicited by nonwords also differ depending on whether they were subsequently remembered or forgotten. In sharp contrast to the effect observed for words, however, subsequently remembered nonwords are associated with a more negative-going ERP than subsequently forgotten nonwords. This effect has a widespread scalp distribution with a focus at central and right temporal sites. It starts around 1 sec after item onset and is largest for a few hundred milliseconds, after which it decreases in size on some electrodes but persists on others.

Figure 3. Neural activity predictive of memory formation for nonwords. Group-averaged ERP waveforms elicited at study by nonsense letter strings that were subsequently remembered versus forgotten. Waveforms are shown for all 29 scalp sites; positive values are plotted upward.
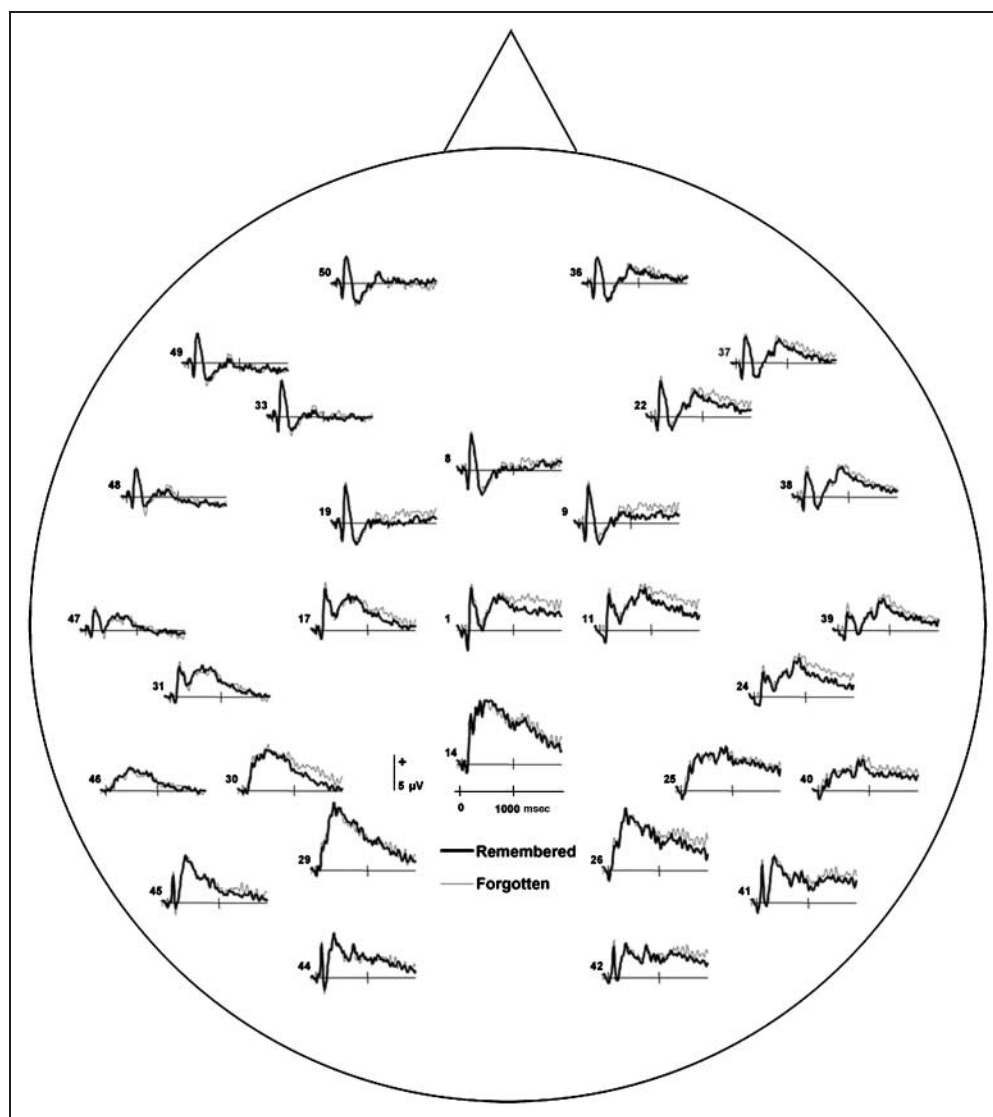
The statistical reliability of the above effects was evaluated by measuring mean amplitudes in the 600–1000, 1000–1400, and 1400–1800 msec time intervals. These intervals were chosen on the basis of the differences visible in the grand-average waveforms and the continuous and long-lasting nature of subsequent memory effects identified in previous encoding studies. The primary analyses focused on the 1000–1400 msec region that exhibited a pronounced subsequent memory effect for both item types, enabling a direct comparison across words and nonwords. The additional analyses on the 600–1000 msec and 1400–1800 msec regions evaluated the earlier and later effects mainly visible for words. Figure 4 illustrates the scalp distributions of the amplitude differences in the three intervals. Mean amplitudes were submitted to repeated-measures analyses of variance (ANOVAs), incorporating the Greenhouse–Geisser correction for violations of sphericity (Keselman & Rogan, 1980). The ANOVAs included factors of item type, subsequent memory performance, and electrode site. These analyses were followed up with planned subsequent memory comparisons for words and nonwords. All 29 available electrode sites were initially entered into the analyses to minimize type I errors that may result from arbitrary selection of sites. However, based on previous work, we a priori expected a frontally distributed, positive-going subsequent memory effect for words; we tested this hypothesis directly with one-tailed t tests on the averaged amplitude across the four frontal electrode sites (sites 36, 37, 49, and 50; www.easycap.de/easycap/e/electrodes/13_M10.htm). We also report the effect on the left frontal site (site 50, roughly equivalent to site Fp1 of the 10/20 system), where the effect is typically largest.

The ANOVA on the 1000–1400 msec region showed a reliable interaction between item type and subsequent memory performance [$F(1, 17) = 7.69$, $p = .013$], not modulated by electrode site. For words, ERP amplitudes differed reliably as a function of an interaction between subsequent memory performance and electrode site [$F(4.9, 83.2) = 2.44$, $p = .042$; F value reported with Greenhouse–Geisser lowered degrees of freedom]. The planned comparison on the four frontal electrode sites confirmed that words that were subsequently remembered were associated with a more positive-going ERP than words that were subsequently forgotten over this region of the scalp [1.0 vs. 0.1 μV; $t(17) = 2.16$, one-tailed $p = .022$]. The same effect was observed when the analysis was restricted to the left frontal site [$t(17) = 1.95$, one-tailed $p = .034$]. For nonwords, a significant main effect of subsequent memory performance

Figure 4. Scalp distributions of observed ERP modulations. Voltage spline maps showing the distribution of the observed ERP differences across the scalp in time windows that formed the basis of the statistical analyses. (A) Distribution of the subsequent memory effects (difference between remembered and forgotten items) for nonwords and words. (B) Distribution of the ERP differences between syllable judgments on nonwords versus words, collapsed across subsequent memory performance. Note that the maps are scaled to the minimum and maximum across all differences to illustrate the distribution as well as size of the modulations.
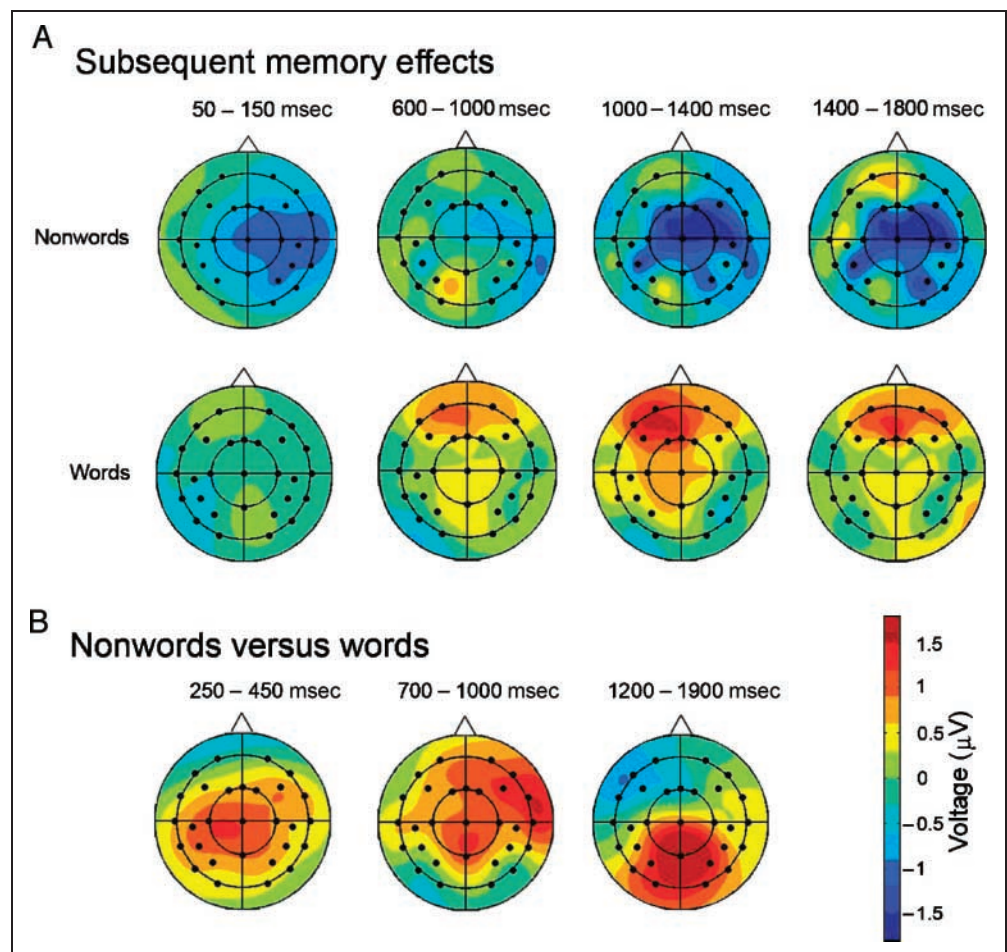
indicated that relative to nonwords that were subsequently forgotten, subsequently remembered nonwords were associated with a more negative-going ERP at study [1.8 vs. 2.5 μV; $F(1, 17) = 9.48$, $p = .007$]. This effect did not vary reliably across the scalp.

The across-item ANOVAs on the 600–1000 and 1400–1800 msec regions did not demonstrate reliable effects involving subsequent memory. However, the direct test for a positive subsequent memory effect for words over the four frontal electrode sites was significant for both latency regions [$t(17) = 2.01$ and 1.94, respectively, one-tailed $p = .030$ and .035]. For the analyses on the left frontal site, the positive-going subsequent memory effect was reliable in the 600–1000 msec region [$t(17) = 1.98$, one-tailed $p = .033$], but just failed to reach significance in the 1400–1800 msec region [$t(17) = 1.71$, one-tailed $p = .053$]. No reliable effects emerged for nonwords.

Early Effect for Novel Items

Unexpectedly, the ERPs for nonwords displayed a very early subsequent memory effect. As illustrated in Figure 5, nonwords that were subsequently remembered elicited a more negative-going ERP almost immediately after their onset relative to nonwords that were subsequently forgotten. This effect seems to surround the N100, and was therefore quantified in the 50–150 msec time window. The across-item ANOVA showed a non-significant trend for an interaction between item type, subsequent memory, and electrode site [$F(4.2, 71.6) = 2.16$, $p = .079$]. However, the separate subsequent memory analyses on each item type showed a reliable main effect of subsequent memory for nonwords [$F(1, 17) = 8.22$, $p = .011$] but not words [$F < 1$].
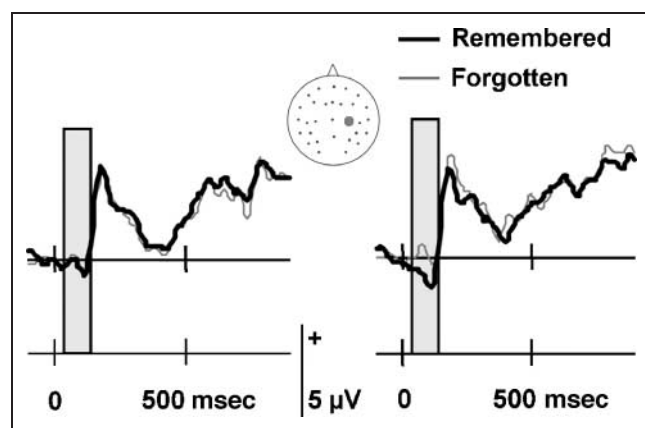

Figure 5. Early subsequent memory effect for nonwords. Group-averaged ERP waveforms from a single electrode site (site 11 of montage 10; www.easycap.de/easycap/e/electrodes/13_M10.htm; equivalent to C4 of the 10–20 system) for words (left) and nonwords (right) that were subsequently remembered versus forgotten. Positive values are plotted upward. For nonwords only, ERP waveforms differed shortly after item onset depending on subsequent memory performance to the item.

Syllable Task ERPs

The final EEG analysis looked at the ERPs elicited by syllable judgments on nonwords versus words irrespective of subsequent memory performance. It has been suggested that the brain supports memory formation by altering some of the processes engaged in service of the ongoing task. That is, successful encoding may be a by-product of on-line processing rather than the result of a dedicated encoding mechanism (Craik & Tulving, 1975; Kolers, 1973; Tulving & Thomson, 1973). This suggestion is, in part, based on the demonstration that the brain regions that demonstrate subsequent memory effects largely overlap with those engaged during the study task on the whole (Fletcher, Stephenson, Carpenter, Donovan, & Bullmore, 2003; Otten, Henson, & Rugg, 2001; Otten & Rugg, 2001a; Wagner, Schacter, et al., 1998). To address a possible relationship between neural activity associated with encoding and task performance in the present experiment, we contrasted the ERPs elicited by syllable judgments on words versus nonwords irrespective of subsequent memory performance. Figure 6 shows the group-averaged waveforms, and Figure 4 the associated spline maps.

Relative to syllable judgments on words, judgments on nonwords elicited a more positive-going ERP over much of the recording epoch. A negative deflection around 350 msec, likely the N400 given its time of occurrence and centro-parietal scalp distribution (Kutas & Federmeider, 2000), was smaller for nonwords. Then, nonwords gave rise to a more positive-going ERP primarily over right frontotemporal sites until at least 1 sec. The largest difference between words and nonwords is visible toward the end of the analysis epoch, when nonwords are associated with a positive-going deflection over mid-parietal sites. The scalp distribution of this difference suggests a contribution of the P300 family of components (Donchin & Coles, 1988).

The reliability of these effects was evaluated by measuring mean amplitudes in the 250–450 msec, 700–1000 msec, and 1200–1900 msec regions, capturing the N400, right temporal, and P300 differences, respectively. Reliable effects involving item type were found for the early and late intervals; the mid-latency differences only approached significance ($p = .085$). The ANOVA on the 250–450 msec region demonstrated a main effect of item type [$F(1, 17) = 4.88$, $p = .04$], indicating that ERPs were more positive for nonwords in this latency region across the scalp. A reliable interaction between item type and electrode site in the 1200–1900 msec region [$F(3.5, 59.7) = 4.62$, $p = .004$] supported the posterior focus of the late positive-going modulation associated with nonwords.

DISCUSSION

The data showed distinct patterns of electrical brain activity during memory formation of nonwords versus words. For words, a positive ERP modulation over frontal scalp

Figure 6. Neural activity associated with making syllable judgments on nonwords versus words. Group-averaged ERP waveforms elicited during the study task by nonwords and words, collapsed across subsequent memory performance. The study task involved the silent counting of the number of syllables in each item in order to decide whether this number was odd or even. Waveforms are shown for all 29 scalp sites; positive values are plotted upward.
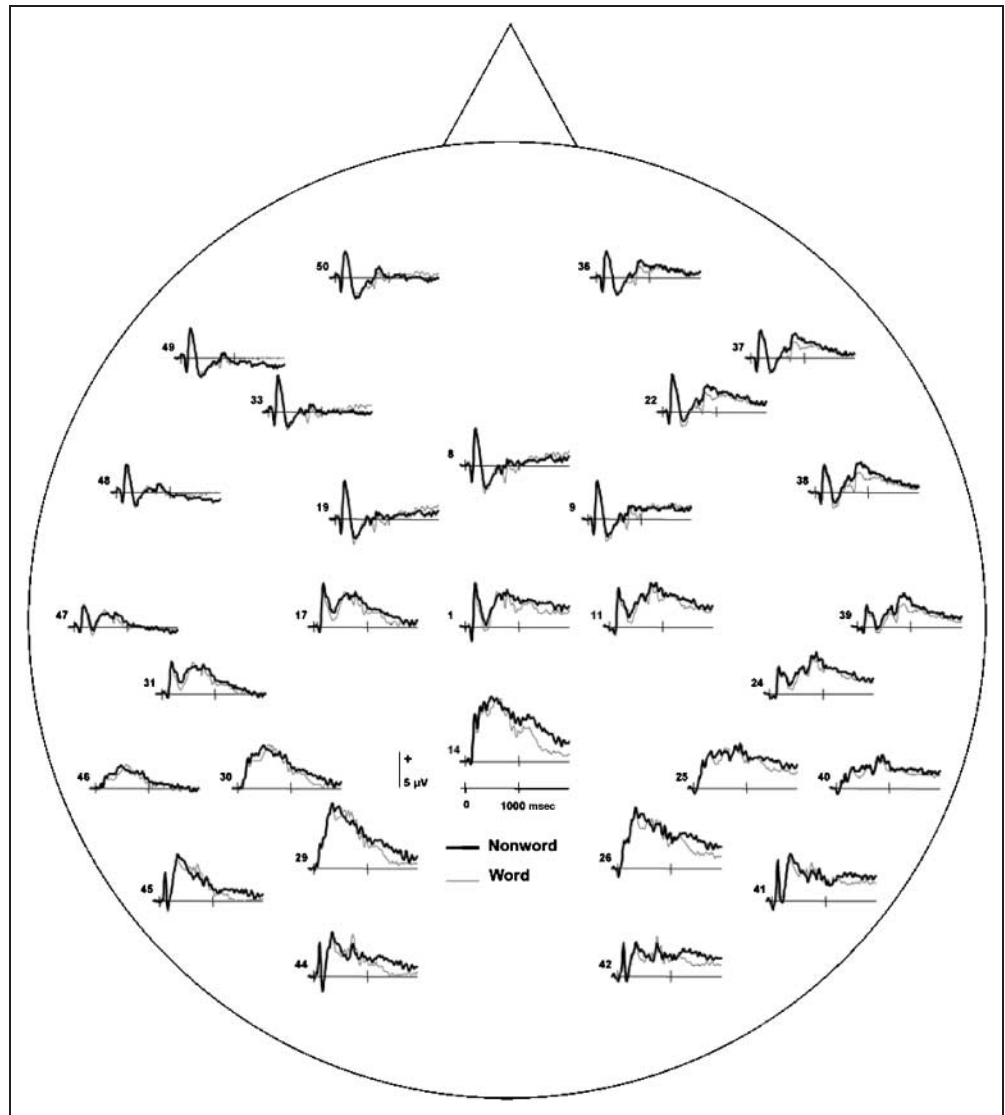
sites predicted encoding success from around 600 msec after word onset. In contrast, the encoding of nonwords was associated with a negative-going, spatially widespread modulation, both shortly after item onset and then again 1 sec later. These findings have two main implications: (i) the brain supports the encoding of familiar and unfamiliar letter strings in qualitatively different ways, including the engagement of distinct neural activity at different points in time, and (ii) the processing of semantic attributes plays a central role in the encoding of familiar information and the associated positive frontal ERP modulation. Below, we discuss these implications in turn.

The primary aim of the experiment was to determine how the brain supports the encoding of information that has not been encountered previously, and therefore, not yet have meaning. This issue was addressed by considering how memories are formed of letter strings that are unfamiliar, but orthographically legal and pronounceable. These strings elicited reliable subsequent memory effects in the ERPs. This implies that the suc-

cessful encoding of this type of string is associated with differential neural activity that can be picked up with scalp-recorded EEG. More important, however, is the observation that the effect for these strings took the form of a widespread negative modulation. This contrasts with the positive modulation over frontal scalp sites typically elicited by meaningful information, including the words in the present experiment.

The polarity of an ERP effect is one aspect of its scalp distribution, and an important indication as to the nature of the neural activity that is engaged (see Otten & Rugg, 2004 or Rugg, 1995 for a description of how to interpret ERP effects). The polarity reversal of subsequent memory effects across nonwords and words indicates that there exists a qualitative, rather than a quantitative, difference in the neural activity associated with encoding these two types of item into long-term memory. The reversal may have arisen because the effects are generated by intracerebral sources with different locations or orientations, or by neurophysiologically

distinct activity (e.g., activity in neuronal populations with excitatory as opposed to inhibitory input, or with input via synapses distal as opposed to proximal to the cell bodies; Wood, 1987). Although it is not possible to infer the exact intracerebral origins of the subsequent memory effects without further evidence, the data indicate that the brain supports the encoding of nonwords and words in qualitatively different ways.

The qualitative neural differences imply that at least one aspect of the cognitive processes associated with memory formation of nonwords and words also differ qualitatively. To understand what cognitive processes are associated with memory encoding in each case, it is necessary to pinpoint the crucial difference between words and nonwords that induced the observed dissociation. The experiment was designed to make the letter strings as comparable as possible, except for their level of familiarity and meaningfulness. It is unlikely that unfamiliarity with the nonsense letter strings per se gave rise to the negative-going modulation. Studies that have looked at the encoding of meaningful items that are less familiar (low- vs. high-frequency words) suggest that, if anything, the positive ERP modulation is larger for such items (Guo et al., 2004; Fernández et al., 1998). Likewise, Neville, Kutas, Chesney, and Schmidt (1986) have shown that sentence-ending words that are unexpected given the preceding sentence evoke a larger positive subsequent memory effect.

It is also unlikely that the observed differences arose because list length and study–test interval were allowed to vary between words and nonwords. This was done to obtain sufficient numbers of remembered and forgotten items in each stimulus category. As explained in the Introduction, past studies have indicated that the positive ERP modulation for meaningful information occurs despite variations in number of experimental items (from tens to a few hundred; compare, e.g., Fernández et al., 1998; Fabiani et al., 1990; Sanquist et al., 1980 with Weyerts et al., 1997; Van Petten & Senkfor, 1996; Paller et al., 1987) and length of study–test delay (from a few minutes to 45 min; compare, e.g., Sommer et al., 1991; Fabiani et al., 1990; Sanquist et al., 1980 with Otten et al., 2006; Otten & Rugg, 2001b) similar to those used here. In addition, the effect occurs regardless of whether the study–test interval is filled with an intervening task (compare, e.g., Fernández et al., 1998; Paller et al., 1987 with Otten & Rugg, 2001b). Thus, these variations are, by themselves, not sufficient to induce a negative-going modulation. If anything, they may have interacted with item type to produce the observed effects.

The most feasible explanation for the qualitatively different subsequent memory effects for words and nonwords is that only the former carries meaning. The nonwords were chosen because they were not derived from existing words (Deacon et al., 2004). This meant that the nonwords could not be analyzed by activating features of related words, such as semantic attributes.

Indeed, nonwords did not elicit the frontal positive ERP modulation thought to signal a more elaborate processing of semantic attributes (Paller & Wagner, 2002; Friedman & Johnson, 2000; Wagner et al., 1999; Rugg, 1995; Paller et al., 1987). They also elicited a smaller N400 (an index of the degree of semantic activation/integration; Kutas & Federmeider, 2000) than words in the present experiment. It could be postulated that nonwords still engaged some level of semantic analysis, as the familiar orthographic and phonological elements may have been sufficient to activate semantic information. However, any such processing would have to be of a qualitatively different kind than that associated with words.

Importantly, the finding of a widespread negative-going ERP modulation during the encoding of nonsense letter strings has recently been replicated (Khader, Ranganath, Seemüller, & Rösler, in press). Khader and colleagues examined the relationship between working and long-term memory with a delayed sample-to-match task and letter strings of the form CVC–CCC (e.g., LITPDR or ZAPTXC). Each string had to be silently rehearsed over a 5–7 sec period in order to make a same/different judgment on a following probe. A recognition memory test incorporating confidence judgments followed. Relative to strings that were later forgotten, strings that were confidently remembered were in the delay period associated with a widespread negative-going ERP modulation with a focus at central sites, similar to the modulation observed in the present experiment. Although no comparison was available with meaningful material, this observation strengthens the idea that items that lack meaning generate qualitatively different subsequent memory effects in ERPs.

What processes are associated with the negative ERP modulation associated with the encoding of nonwords? One possibility is that the effect reflects the degree to which phonological attributes are processed. Overall, syllable judgments on nonwords took longer than those on words, suggesting that phonological processing was more extensive for nonwords. Given the absence of semantic attributes, memory formation for nonwords may have relied on across-item differences in the degree of phonological analysis, which increases the likelihood that a lasting memory is formed from an event (Craik & Lockhart, 1972).

Several lines of evidence argue against an explanation of the effect in terms of phonological analysis. First, the relatively late onset of the effect (around 1 sec) does not fit the typical time course of phonological processing (around 400 msec; e.g., Van Turennout, Hagoort, & Brown, 1998). Second, if subsequently remembered and forgotten nonwords received different amounts of phonological processing at study, it might be expected that the time needed to give a syllable judgment to each differed as well. This was not the case. Third, if the negative ERP modulation reflected phonological processing,

it might be expected that a similar modulation differentiated syllable judgments on nonwords versus words. This, too, was not the case. Fourth, the nonwords used in the Khader et al. (in press) study were orthographically illegal and unpronounceable, yet generated a similar negative-going effect. Finally, in ERP studies that have looked at subsequent memory effects in phonological judgment tasks (Paller et al., 1987; Sanquist et al., 1980), a positive-going, not negative-going, effect was observed.

Instead of phonological processing, the negative ERP subsequent memory effect may reflect the maintenance and manipulation of object-related information in working memory. Sustained negative ERP deflections with widespread scalp distributions have been observed in delayed match-to-sample tasks that require the comparison of visual objects (see Ruchkin, Grafman, Cameron, & Berndt, 2003, for a review). These deflections are thought to be associated with the requirement to keep object-related information in working memory. In the present case, some nonwords, but not others, may have been stored in memory because their visual image resulted in an internal representation that was created or maintained more efficiently. This may have aided subsequent processing of the letter string. It is noteworthy that in a previous study that emphasized orthographic as opposed to semantic processing, a negative-going modulation similar to the one observed here was found (Otten & Rugg, 2001b). Words may not elicit this negative-going modulation (though see Mangels, Picton, & Craik, 2001, for an exception) because meaning-related processing takes precedence over object-related processing.

Intriguingly, nonwords elicited a reliable subsequent memory effect not only late in the epoch but also shortly after item onset. This effect has to be interpreted with caution, as it was unexpected and only approached statistical significance in the between-item comparison. Inspection of the ERP waveforms time-locked to the onset of the prestimulus cue suggested that the effect did not originate before stimulus onset. Instead, it may reflect the benefit to memory of an increased level of attention to nonwords, which would be expected to modulate early ERP components including the N1 (Mangun & Hillyard, 1995). Increased attention to a visual image on the screen may result in an internal representation that can be maintained and processed more efficiently.

For nonwords as well as words, the present data do not provide evidence that encoding-related activity necessarily overlaps with activity related to task performance on the whole (cf. Fletcher et al., 2003; Otten et al., 2001, 2002; Wagner, Schacter, et al., 1998). The ERP modulations that differentiated items that were subsequently remembered versus forgotten were not identical to the modulations that differentiated syllable judgments on words versus nonwords. Thus, at least in the present circumstances, memory formation may have been supported by neural mechanisms that were additional to those required for the syllable task, or common to syllable judgments on words and nonwords.

A limitation of the present subsequent memory analyses concerned the need to collapse study trials across remember and know judgments. This prevented an assessment of whether the observed ERP effects should be attributed to encoding-related activity that supports later recollection, familiarity, or both. Importantly, however, the observed qualitative differences across subsequent memory effects for words and nonwords cannot be explained by the need to collapse trials. The behavioral analyses indicated that although memory was better for words on the whole, words and nonwords were equally likely to be remembered on the basis of recollection and familiarity. Thus, the probability that a study trial engaged activity associated with later recollection versus familiarity was the same for both item types. In this respect, it is noteworthy that Khader et al. (in press) observed a negative-going modulation for nonwords when the analyses were restricted to confident hits.

The secondary aim of the experiment was to shed light on the functional significance of the positive frontal subsequent memory effect usually observed for meaningful material (Paller & Wagner, 2002; Friedman & Johnson, 2000; Rugg, 1995). The fact that this modulation was only elicited by words strongly suggests that the processing of orthographic and phonological attributes, both of which were also contained within nonwords, is not sufficient to elicit the modulation. Instead, the effect must reflect the processing of meaning-related attributes, or processes contingent on this, such as associative features. These findings thus constrain the suggested functional interpretation of the positive subsequent memory effect (Friedman & Johnson, 2000; Wagner et al., 1999; Van Petten & Senkfor, 1996; Paller et al., 1987). The processing of semantic attributes must play a role in the elicitation of this effect, and, by inference, the creation of long-term memories from meaningful information (cf. Craik & Lockhart, 1972).

The positive modulation was elicited although the study task did not require the processing of semantic attributes. Subjects were asked to decide whether each item had an odd or even number of syllables, a judgment that can be made on the basis of phonological information alone. The odd/even decision may have been aided by knowing a word's meaning (Patterson & Coltheart, 1987), or the opportunity to elaborate on the meaning of a word may have arisen after the odd/even decision was made. On this account, the positive modulation occurred because semantic processes incidental to the task at hand were engaged. The same argument has been made for activations in the left prefrontal cortex during nonsemantic study tasks (Otten et al., 2001). The incidental nature of semantic processing explains the relatively modest size of the positive modulation in the present experiment.

In conclusion, qualitatively different ERP subsequent memory effects were observed for words and nonsense letter strings. Although the precise functional interpretation of these effects cannot be established on the basis of the present data alone, the polarity and time-course differences allow the strong conclusion that the brain supports memory formation in different ways depending on whether an item carries meaning. This includes the engagement of distinct neural activity at different points in time. It will be of interest to identify what brain regions underlie the effects observed on the scalp. Not only will this pinpoint the brain systems associated with laying down memories for different kinds of items, it will also help elucidate the functional role of neural activity associated with the encoding of items devoid of meaning.

Acknowledgments

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