Study–Test Congruency Affects Encoding-related Brain Activity for Some but Not All Stimulus Materials

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Abstract

■ Memory improves when encoding and retrieval processes overlap. Here, we investigated how the neural bases of long-term memory encoding vary as a function of the degree to which functional processes engaged at study are engaged again at test. In an incidental learning paradigm, electrical brain activity was recorded from the scalps of healthy adults while they made size judgments on intermixed series of pictures and words. After a 1-hr delay, memory for the items was tested with a recognition task incorporating remember/know judgments. In different groups of participants, studied items were either probed in the same mode of presentation (word–word; picture–picture) or in the alternative mode of presentation (word–picture; picture–word). Activity over anterior scalp sites predicted later memory of words, irrespective of type of test probe. Encoding-related activity for pictures, by contrast, differed qualitatively depending on how an item was cued at test. When a picture was probed with a picture, activity over anterior scalp sites predicted encoding success. When a picture was probed with a word, encoding-related activity was instead maximal over posterior sites. Activity differed according to study–test congruency from around 100 msec after picture onset. These findings indicate that electrophysiological correlates of encoding are sensitive to the similarity between processes engaged at study and test. The time course supports a direct and not merely consequential role of encoding–retrieval overlap in encoding. However, because congruency only affected one type of stimulus material, encoding–retrieval overlap may not be a universal organizing principle of neural correlates of memory. ■

INTRODUCTION

The ability to remember specific events from daily life depends on the degree to which the circumstances surrounding the initial encoding of an event resemble those surrounding its later retrieval. The more similar encoding and retrieval processes are, the more likely it is that the event will be remembered. For example, Morris, Bransford, & Franks (1977) demonstrated that memory performance following semantically encoded words is best when the retrieval cue emphasizes semantic processing. Performance for phonologically encoded words, by contrast, is best when phonological processing is emphasized. In a similar vein, studies have shown that memory is better when items are presented in the same physical format at study and test (e.g., Mulligan & Osborn, 2009; Mintzner & Snodgrass, 1999; Weldon & Roediger, 1987). Findings such as these have led to the "encoding specificity" (Tulving & Thomson, 1973) and "transfer-appropriate processing" (Roediger, 1990) theoretical frameworks. On these accounts, memory not only depends on the type and amount of processing engaged at encoding (Craik & Lockhart, 1972) but also on the interaction between encoding and retrieval processes. When encoding processes are recapitulated at test, there is an increased probability that a test probe will make contact with a stored representation. As a consequence, memory is better (for a review, see Craik, 2002).

Despite the evidence that study–test congruency impacts memory performance, studies investigating the neural bases of human memory have not yet considered the role of study–test congruency in great detail (Rugg, Johnson, Park, & Uncapher, 2008). Study–test congruency has been studied in the light of neural models that stipulate that retrieval success depends on the reinstatement of neural activity engaged when an event was initially encountered (Norman & O'Reilly, 2003; Rolls, 2000; Alvarez & Squire, 1994). These models share many features with the psychological frameworks outlined above. In support of such models, a handful of neuroimaging studies have shown that brain regions involved in the encoding of information are indeed reinstated during the retrieval of that information (Johnson, McDuff, Rugg, & Norman, 2009; Johnson & Rugg, 2007; Wheeler et al., 2006; Vaidya, Zhao, Desmond, & Gabieli, 2002; Nyberg, Habib, McIntosh, & Tulving, 2000; Wheeler, Buckner, & Peterson, 2000).

A related, but different, question is how congruency in functional processes across study and test affects encoding-related activity. This question focuses on delineating the nature and timing of encoding-related brain activity rather than identifying overlap in neural processes across study and test. This question is important not only because of

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its theoretical significance but also because it allows a better understanding of differences in encoding-related activity seen across, for example, individuals and the lifespan.

Little empirical work has been directed at the question of how study–test congruency affects encoding-related activity. Previous work has demonstrated that there is not a single type of brain activity that is associated with effective encoding under all circumstances. Encoding-related activity differs depending on the type of material that is stored into memory (Uncapher & Rugg, 2009; Paller & Wagner, 2002; Kirchhoff, Wagner, Maril, & Stern, 2000; Wagner, Koutstaal, & Schacter, 1999) and the type of processing engaged when that information is encountered (Mitchell, Macrae, & Banaji, 2004; Davachi, Mitchell, & Wagner, 2003; Fletcher, Stephenson, Carpenter, Donovan, & Bullmore, 2003; Baker, Sanders, Maccotta, & Buckner, 2001; Otten & Rugg, 2001a, 2001b). This has led to the suggestion that encoding is a by-product of whatever operations are ongoing in the course of a study task (Otten & Rugg, 2001b). This is in general agreement with the transfer-appropriate processing framework (Craik, 2002; Kolers, 1973; Craik & Lockhart, 1972). One of the premises of this framework is that the particular attributes that are focused on during encoding determine the nature of the representation of an event in memory. Encoding-related brain activity is expected to differ as a consequence. Another premise is that retrieval of an event is facilitated when the retrieval cue matches attributes in a stored representation to a greater degree. Different retrieval cues tap into different representations to different degrees, depending on their similarity. It would, therefore, be expected that encoding-related activity differs not only as a function of the attributes that are attended during encoding but also those used during retrieval.

A few studies have indeed shown that neural correlates of encoding vary, depending on the circumstances surrounding retrieval. Otten (2007) recorded event-related fMRI signals while participants made size judgments on visually presented words. Memory for the words was probed with either a spoken word cue or a picture cue. Activity in different sets of brain regions predicted encoding success, although the circumstances surrounding encoding were identical. A similar finding was reported by Bridger and Wilding (2010), who used electrical brain activity to investigate the influence of retrieval requirements on encoding-related activity. Participants performed one of two incidental encoding tasks on words presented at left and right of fixation. Across different test blocks involving physically identical cues, participants were asked to recover either the screen location or encoding task associated with a studied word. Qualitatively different brain activities were associated with encoding success in each case. It was proposed that the particular activity observed at encoding reflects the processing of those stimulus attributes that are used to restore a representation. Finally, several studies have shown that encoding-related activity

varies according to whether responses at test are associated with recollection or familiarity (Ranganath et al., 2004; Davachi et al., 2003) or with explicit or implicit memory (Schott et al., 2006; Schott, Richardson-Klavehn, Heinze, & Düzel, 2002). Thus, the type of memory judgment affects encoding-related activity.

The above studies demonstrate that the circumstances surrounding retrieval influence the type of brain activity that is observed for effective encoding on any occasion. However, they do not determine whether it is the type of retrieval cue or the degree of congruency in functional processes across study and test that defines the nature of encoding-related brain activity. This was the purpose of the present study. We aimed to assess how degree of congruency between a studied event and a test cue influences encoding-related brain activity. This question has only been addressed in a previous fMRI study. Park and Rugg (2008) used fMRI to assess how overlap between modes of presentation of study and test items affects brain regions associated with encoding. Participants made indoor/outdoor judgments on intermixed series of pictures and words. For both item types, memory was assessed with a remember/know recognition task using cues in the same or alternative mode of presentation (Tulving, 1985). Whether encoding-related activity was sensitive to degree of congruency was considered by pinpointing regions where fMRI signals associated with the on-line processing of a stimulus class were greater when items were later remembered with congruent than incongruent cues. For both words and pictures, several such regions were found when the data were collapsed across remember and know judgments. Although the analysis approach only considered a subset of all encoding-related activity, these data suggest that at least some encoding processes are sensitive to the degree of functional overlap across study and test.

The slow temporal dynamics of hemodynamic brain activity limits the kind of conclusions that can be drawn from fMRI. In the case of encoding-related activity, it is not clear at what point in time differences as a function of study–test congruency emerge. This is important because activity that is directly associated with the creation of a representation in memory is expected to be involved shortly after event onset (Cameron, Yashar, Wilson, & Fried, 2001). If effects of study–test congruency emerge late, they may be a consequence, rather than cause, of encoding (cf. Rugg et al., 2008). In the present experiment, we employed the high temporal resolution of electrical brain activity to discern the impact of study–test congruency on the timing as well as nature of encoding-related activity. We manipulated the similarity between encoding and retrieval processes by changing the perceptual similarity of study and test events. The Park and Rugg (2008) study described above has documented the effectiveness of this procedure and memory performance is known to benefit when modes of presentation match across study and test (e.g., Schloerscheidt & Rugg, 2004; Mintzner & Snodgrass, 1999).

Healthy adults made size judgments about series of intermixed words and pictures. After a delay, memory for the items was tested with a recognition task. Crucially, some study items were cued in the same mode of presentation at test (word–word; picture–picture), whereas others were cued in the alternative mode (word–picture; picture–word). Study–test congruency was manipulated across two groups of participants. A between-subjects design was used to obtain sufficient numbers of remembered and forgotten to use the subsequent memory procedure explained below. Pilot work indicated that few pictures would be forgotten when probed with pictures in a within-subjects design. In Park and Rugg (2008), this condition was, on average, associated with only seven forgotten items (see their Table 2). A between-subjects design offered greater trial numbers and the potential for increased statistical sensitivity.

The recognition task incorporated remember/know judgments (Tulving, 1985) to separate different sources that may underlie recognition. Although this procedure is not process pure and subject to other limitations (e.g., Wais, Mickes, & Wixted, 2008; Yonelinas, 2002), it allowed us to limit the possibility that comparisons of encoding-related activity were confounded by type of recognition judgment. By restricting the analyses to remember judgments, any differences observed as a function of study–test congruency cannot easily be attributed to differences in the type of recognition judgment a study item later received. In addition, subsequent memory effects tend to be larger for items later given remember judgments (Paller & Wagner, 2002).

Brain activity associated with successful encoding was assessed with the "subsequent memory" approach (Sanquist, Rohrbaugh, Syndulko, & Lindsley, 1980). This is a powerful procedure to isolate activity specifically related to memory from other ongoing cognitive processes. In the approach, activity recorded at study is sorted depending on whether an event is remembered or forgotten in a later memory test. Study activity that differs as a function of subsequent memory performance is taken to be relevant for encoding (for a review, see Paller & Wagner, 2002). The question of interest was how encoding-related activity varies depending on congruency in presentation modes across study and test. One possibility is that the same activity is engaged under all circumstances, albeit perhaps to different degrees. Such activity would signal encoding processes that are germane to any event, irrespective of how its representation is later retrieved. Alternatively, items whose distinguishing features are processed more extensively at study may benefit most from a retrieval cue in the same physical format. For example, items whose semantic attributes are emphasized during encoding may benefit from a retrieval cue in the form of a word. This type of encoding may be more likely when the study event also consists of a word. Likewise, study items whose physical attributes receive preferential processing may overlap more with a picture cue. This type of encoding may suit pictures best. Although

scalp-recorded electrical brain activity does not easily allow a determination of intracranial neural sources (Nuñez, 1981), differences in the distribution of activity across the scalp signal qualitative differences in the neural and cognitive processes that are involved in encoding (Otten & Rugg, 2005). With respect to timing, encoding-related activity was expected to start soon after a study event was encountered. If study–test congruency affects encoding directly, its influence would be expected to materialize at about the same time.

METHODS

Participants

The experimental procedures were approved by the University College London Research Ethics Committee. Forty-eight native English speakers were remunerated at £7.50/hr for taking part in the experiment. All reported to be right-handed, to have normal or corrected-to-normal vision, and to be free from neurological and psychiatric histories. Color vision was checked with abridged Ishihara plates. Participants were randomly assigned to one of two groups: the "match" group ($n = 24$, 15 women, mean of age = 23 years, range = 19–34 years) or the "mismatch" group ($n = 24$, 15 women, mean of age = 23 years, range = 18–34 years). The data from a further 11 volunteers were excluded from the analyses because of uncorrectable eye movements or fewer than 14 remembered or forgotten trials in each relevant condition. All participants provided written informed consent.

Stimulus Material

Stimuli were drawn from a pool of 411 everyday objects and animals (see Figure 1 for examples). Each item was available in the form of a picture and the form of a word. Pictures were grayscale photographs from the Hemera Photo Objects suite. Words depicted the names of the item and were between 3 and 11 letters in length. Three sets of 128 items each were selected pseudorandomly from the pool with the restrictions that word lengths would be approximately equal across sets and that half of the images in each set represented items that in their actual size could fit into a shoebox. The sets were rotated across participants such that each item was presented equally often as a picture or a word and as a studied or unstudied item. Two of the sets were used to create a study list of 256 critical items. This list consisted of 128 words and 128 pictures, which were randomly intermixed. Four filler items were added to the beginning of the list. These were not considered in the analyses. All three item sets were used to create a test list of 384 critical items. This list contained all 256 studied items and the 128 items not yet encountered in the experiment (64 words and 64 pictures). The first six items in the test list were filler items.
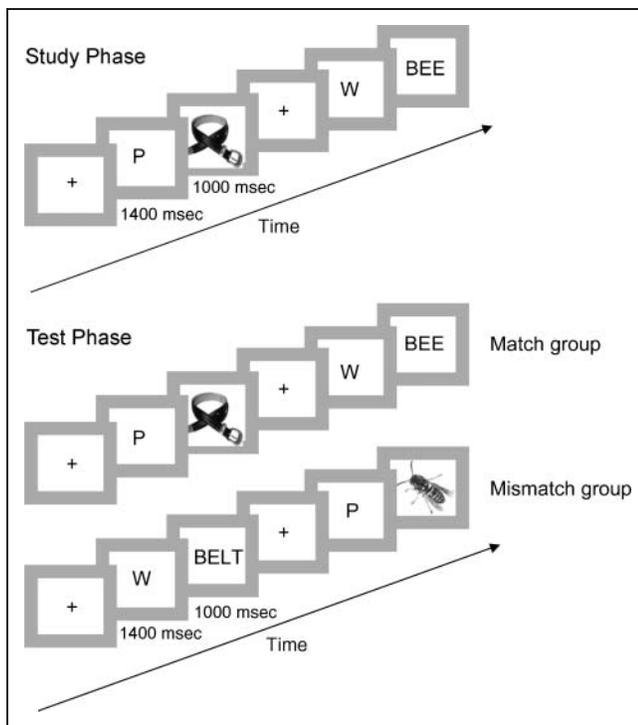
Figure 1. Sequence of events during the study and test phases of the experiment. Participants saw sequences of randomly intermixed pictures and words. A cue before item onset indicated the mode of presentation of the upcoming item. The study phase consisted of an incidental encoding task (size judgments) on all items. At test, a recognition memory task incorporating remember/know judgments was performed. Participants in the match group saw old items in the same mode of presentation as during study (word–word; picture–picture). Participants in the mismatch group saw old items in the alternative mode (word–picture; picture–word).

The crucial manipulation consisted of the correspondence between the modes of presentation of study and test items. In the match group, studied items were shown in the same mode at test (i.e., picture–picture; word–word). In the mismatch group, studied items were shown in the alternate mode (i.e., picture–word; word–picture). Study and test lists were split into blocks of 64 items to allow short rest breaks. New random sequences were generated for each participant. The remaining items in the pool were used for practice lists.

Experimental Procedure

The experiment consisted of an incidental encoding task, followed by a surprise recognition memory test after a 1-hr delay. At study, participants saw a series of words and pictures, presented one at a time. Words and pictures were equally likely to occur and randomly intermixed. Each item was preceded by the letter "W" or "P," which served as a cue to indicate whether a word or picture would be presented next. Participants were encouraged to use the cue to prepare for the upcoming item. The task was to decide whether the item could, in its actual size, fit into a shoebox.

Participants pressed one of two buttons with their left or right index fingers according to their decision. Both speed and accuracy were stressed. Responding hand was counterbalanced across participants. The study phase started with a short practice list, followed by four task blocks. This phase lasted around 25 min.

Participants then rested while conversing with the experimenter or reading a book. After 1 hr, participants were informed that their memory for the items from the shoebox task would be tested. Participants were given a new series of intermixed pictures and words, some of which had occurred in the shoebox task and some of which were new to the experiment. The letter "W" or "P" was again shown before each item to indicate that a word or picture would be viewed next. For each item, participants had to make a "remember," "know," or "new" judgment (Tulving, 1985) by pressing one of three buttons with their right index, middle, or ring finger. If participants were confident that they had seen an item before and could recollect one or more details from the initial encounter with the item, they had to give a remember response. If they were confident that the item had occurred earlier but could not recollect any details, a know response had to be given. Finally, if they thought that the item had not occurred in the experiment, they had to give a new response. To avoid contamination of hits by lucky guesses, participants were asked to also press the new button when they were not confident about their decision (cf. Park & Rugg, 2008). In both the match and mismatch groups, the instructions emphasized that the memory judgments should be made irrespective of whether an item had occurred as a picture or a word in the shoebox task. The mapping of response finger to recognition judgment was randomized across subjects. Both speed and accuracy were stressed. The test phase started with a brief practice block, followed by six task blocks of 64 trials each. The phase lasted around 1 hr.

At both study and test, stimuli were shown on a computer monitor in central vision on a white background. A black Helvetica font was used for word stimuli and a red font for letter cues. Pictures and words were shown for 1 sec and subtended approximate visual angles of $1.6 \times 1.6°$ and $1–2.9 \times 0.3°$, respectively. Cues appeared 1.5 sec before item onset and remained visible throughout the cue interval except for the final 100 msec, when the screen went blank. Cues subtended $0.3° \times 0.3°$ of visual angle. At study, the time between item offset and the onset of the next cue varied randomly between 1.5 and 3 sec. At test, this time varied between 2.5 and 4 sec. A fixation cross (a plus sign) was visible throughout the tasks, except when cues and items were presented.

EEG Acquisition

Electrical brain activity was recorded from 32 scalp sites using silver/silver-chloride electrodes fitted in an elastic cap according to an equidistant electrode montage (Montage 10 at www.easycap.de/easycap/e/electrodes/

13_M10.htm). Two additional electrodes were placed on the right and left mastoids. Vertical eye movements were recorded bipolarly from electrodes above and below the right eye. Horizontal eye movements were recorded from electrodes placed at the outer canthi. All data were recorded relative to a midfrontal site. Impedance was kept below 5 kΩ. Signals were amplified, band-pass filtered between 0.01 and 35 Hz (3 dB roll-off), and digitized at a rate of 500 Hz with 12-bit resolution.

Data Analysis

Memory Test

The accuracy with which old items could be discriminated from new items was initially assessed across all old responses. We present signal detection (d') and two-high threshold (Pr; Snodgrass & Corwin, 1988) measures of discrimination accuracy in light of the uncertainties surrounding the best way to quantify recognition memory data. Pr was computed by subtracting the proportion of new items incorrectly endorsed as old from the proportion of old items correctly endorsed as old. Classic signal detection theory was used to compute d' measures of sensitivity (Macmillan & Creelman, 2004). Pr and d' showed the same pattern of results. Because the analyses of electrical brain activity focused on remember judgments, Pr was also computed for remember judgments in isolation.

EEG Data

Off-line, the EEG data were digitally filtered between 0.05 and 20 Hz (96 dB roll-off, zero phase shift filter) to remove low- and high-frequency noise. The data were then downsampled to 125 Hz and algebraically re-referenced to averaged mastoids, reinstating the on-line reference site. Epochs of 2048-msec duration surrounding picture and word onsets were extracted from the data recorded during the study phase. Epochs included a 100-msec period before item onset, which was used as the baseline. ERP waveforms were created for each subject and electrode site by averaging epochs containing words or pictures given remember, know, and new judgments in the later recognition memory test. ERPs were corrected for blink artifacts with a standard regression technique (Rugg, Mark, Gilchrist, & Roberts, 1997). Epochs including drifts exceeding ±50 μV, horizontal eye movements, muscle artifacts and amplifier saturations were excluded from the averaging process. ERPs were based on a minimum of 14 artifact-free trials in each condition.

To investigate how study–test congruency affects encoding-related brain activity, subsequent memory effects (Sanquist et al., 1980) were contrasted across the match and mismatch groups. These analyses focused on activity elicited by studied pictures and studied words that were given remember versus new judgments in the subsequent

recognition test. As explained in the Introduction, restricting the analyses to remember judgments ensured that encoding-related comparisons were not confounded by differences in type of recognition judgment. Only a subset of participants had at least 14 artifact-free trials for items given know judgments (17 in the mismatch group and 20 in the match group), and this response category was, therefore, not considered in isolation. For completeness, we also analyzed the data by collapsing remember and know responses. These analyses showed the same pattern of results as we report in the manuscript, except that the effects were smaller and statistically weaker.

ERP waveforms were quantified by measuring mean amplitude values in selected latency regions. The statistical reliability of amplitude and scalp distribution differences was established with mixed-design ANOVAs. The initial ANOVA incorporated the between-subjects factor of group (match/mismatch) and the within-subjects factors of item type (word/picture), subsequent memory (remembered/forgotten), and electrode site. Significant interactions involving subsequent memory were followed up with subsidiary analyses to understand the nature of the interaction. Only effects involving subsequent memory will be reported. For factors with more than two levels, the reported p values and degrees of freedom were adjusted according to the Greenhouse–Geisser correction for nonsphericity (Keselman & Rogan, 1980). Unless specified otherwise, all 32 electrode sites were entered into the analyses. Significant interactions involving electrode sites were followed by analyses on scaled data to establish reliable scalp distribution differences (McCarthy & Wood, 1985). Although scaling has been debated in the literature (Urbach & Kutas, 2002, 2006; Haig, Gordon, & Hook, 1997), some form of scaling is necessary to solve the incompatibility between the additive ANOVA model and multiplicative ERP data (Wilding, 2006; Ruchkin, Johnson, & Friedman, 2003). Here, we used the max/min scaling method to equate amplitudes of subsequent memory effects across conditions and groups because of the interpretational problems that have been noted with vector scaling (Urbach & Kutas, 2002, 2006; Wilding, 2006; Haig et al., 1997). We report results on scaled as well as unscaled data.

RESULTS

Behavioral Data

Encoding Task

Size judgments on pictures took, on average, 841 msec ($SD = 136$ msec) in the match group and 811 msec ($SD = 151$ msec) in the mismatch group. For words, these times were 830 msec ($SD = 106$ msec) and 814 msec ($SD = 151$ msec), respectively. An ANOVA contrasting mean response times across groups and item types did not reveal significant differences, $ps > .316$. Response times also did not differ when items were separated according to later

memory performance, $ps > .072$. Accuracy of size judgments was not considered because of the subjective nature of the judgment for many items.

Memory Test

Recognition memory performance is listed in Table 1. Collapsed across remember and know judgments, *Pr* was 0.58 and 0.43 for words in the match and mismatch groups, respectively. For pictures, these values were 0.59 and 0.47. An ANOVA comparing *Pr* across groups and item types revealed a significant main effect of Group, $F(1, 46) = 20.01$, $p < .0001$, other $ps > .360$. This indicated that participants were more accurate discriminating old from new items when the physical format of items matched across study and test. The same result was obtained when recognition performance was quantified with d' measures. The d' values for words were 1.75 and 1.11 in the match and mismatch groups, respectively. For pictures, these values were 1.80 and 1.20. An ANOVA again resulted in a significant main effect of Group, $F(1, 46) = 30.64$, $p < .0001$. Response times for old judgments did not show significant differences, $p > .105$. When the analyses were restricted to remember responses, no significant differences emerged in *Pr*, $p > .062$. Remember responses were generally given more rapidly for words, $F(1, 46) = 4.57$, $p = .038$, and when items were cued in the same mode of presentation at test. The latter just failed to reach statistical significance, however, $F(1, 46) = 4.03$, $p = .051$.

Encoding-related Brain Activity

Figure 2 shows the group averaged ERP waveforms for study items that were later remembered or forgotten with congruent and incongruent test cues. For words, re-membered items exhibited a small positive-going modulation over frontal scalp sites in the middle of the analysis epoch, regardless of whether the test cue consisted of a picture or a word. For pictures, later remembered items also elicited a positive-going modulation over frontal scalp sites. This effect had an early onset of around 100 msec and was larger and more sustained than the effect visible for words. Importantly, this effect only emerged when pictures were later probed with pictures. In striking contrast, when pictures were probed with words, a positive-going modulation over posterior scalp sites was evident. Similar to congruent cues, encoding-related activity emerged at around 100 msec and persisted throughout the epoch. These observations were confirmed by the statistical analyses. Subsequent memory effects were quantified by measuring mean amplitude values in the 100–700, 700–1300, and 1300–1900 msec intervals. These intervals capture the sustained effects visible for pictures and allow an assessment of the smaller effect for words in the middle latency region. Although picture-related activity was evident throughout the 100–1900 msec period, separating the epoch into three intervals enabled the evaluation of possible differences over time. None of the comparisons across intervals revealed significant differences over time, and only the effects in each interval are, therefore, reported.

Table 2 presents the statistics associated with the comparisons of ERP amplitudes across conditions in each analysis interval. The ANOVAs revealed significant four-way interactions between Item Type, Group, Subsequent Memory, and Scalp Location in all three intervals. The interaction in the first interval remained significant after scaling the data to equate amplitudes across conditions, $F(3.7, 170.3) = 2.69$, $p = .037$. Subsidiary analyses were performed on each item type to understand the nature of this interaction. For words, none of the interactions involving Group, Subsequent Memory, and Scalp Location reached

Table 1. Recognition Memory Performance for Words and Pictures Cued in the Same Mode of Presentation at Test (Match Group) and in the Alternative Mode of Presentation (Mismatch Group)

Group	Item Type	Proportion of Responses			Mean Response Times (msec)		
		Remember	Know	New	Remember	Know	New
Match	Old word	0.43 (0.14)	0.32 (0.15)	0.25 (0.08)	976 (195)	1161 (312)	1098 (293)
	Old picture	0.40 (0.14)	0.31 (0.16)	0.29 (0.11)	997 (239)	1141 (314)	1078 (278)
	New word	0.03 (0.03)	0.13 (0.10)	0.84 (0.11)	840 (544)	1157 (420)	1032 (245)
	New Picture	0.04 (0.03)	0.09 (0.06)	0.87 (0.07)	790 (528)	1115 (519)	1020 (262)
Mismatch	Old word	0.44 (0.16)	0.22 (0.13)	0.34 (0.14)	1130 (243)	1347 (346)	1367 (384)
	Old picture	0.39 (0.15)	0.25 (0.12)	0.36 (0.14)	1094 (204)	1315 (337)	1258 (334)
	New word	0.08 (0.08)	0.15 (0.11)	0.77 (0.16)	954 (518)	1315 (444)	1190 (282)
	New Picture	0.09 (0.07)	0.18 (0.12)	0.73 (0.14)	1044 (436)	1313 (446)	1304 (336)

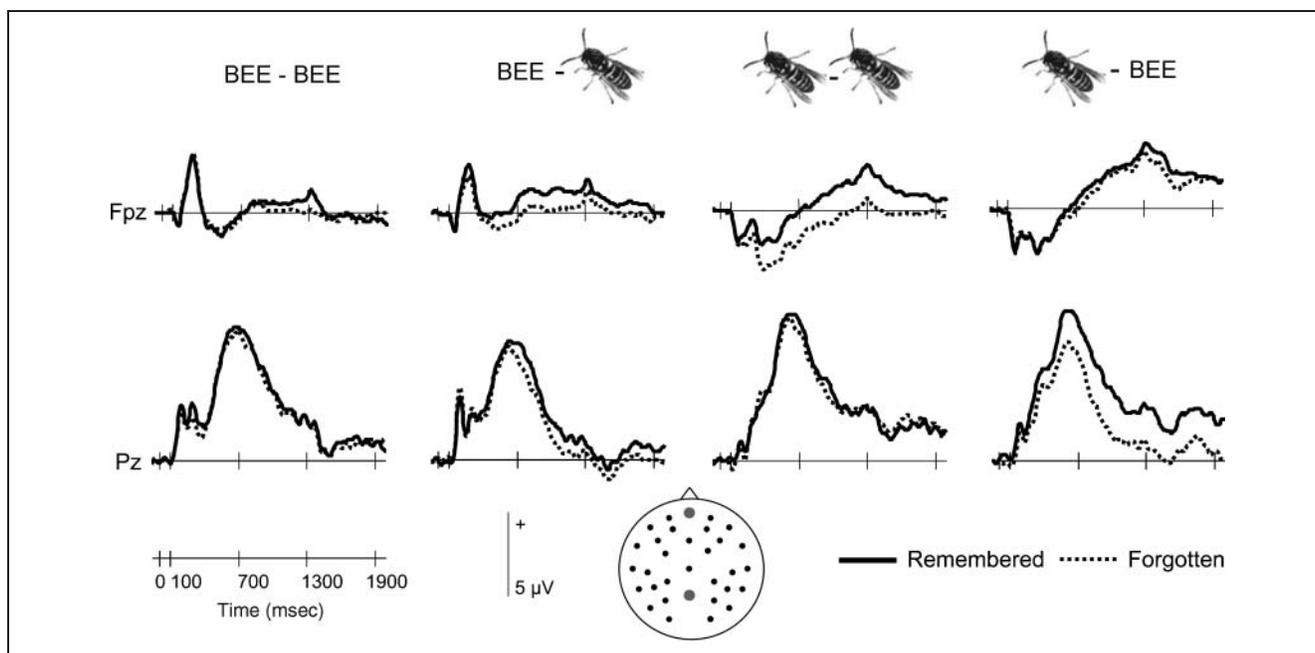Values are across-subject means (*SD*).

Figure 2. Encoding-related neural activity. Group averaged ERP waveforms elicited at study by words and pictures cued in the same mode of presentation (match group) and different mode of presentation (mismatch group). Waveforms are overlaid according to whether an item was later remembered (given a remember judgment) or forgotten (given a new judgment). Waveforms are shown for two representative midline electrode sites (equivalent to Fpz and Pz of the international 10/10 system). Positive values are plotted upward.

significance, $ps > .476$. However, a significant main effect of Subsequent Memory was found in the 700–1300 msec interval, $F(1, 46) = 6.93, p = .012$. Although the interaction between Subsequent Memory and Electrode Site only approached significance ($p = .064$), a direct test to establish the presence of the subsequent memory effect typically observed in deep encoding tasks (Otten, Sveen, & Quayle, 2007; Friedman & Johnson, 2000) confirmed that later remembered words gave rise to more positive-going waveforms over the five most anterior electrode sites than words that were later forgotten, $F(1, 46) = 7.68, p = .008$. Figure 3 shows the corresponding spline maps.

For pictures, significant interactions emerged between Group, Subsequent Memory, and Scalp Location in all three time intervals (Table 2). These interactions were still observed after scaling the data, $F(3.9, 180.4) = 6.61$, $F(5.0, 231.2) = 8.34$, and $F(4.5, 206.2) = 6.86$ for the 100–700, 700–1300, and 1300–1900 msec intervals, respectively, all $p < .0001$. Table 3 lists the results of subsidiary analyses in the match and mismatch groups. In both groups, all three latency regions showed significant interactions between subsequent memory and electrode site. These interactions remained significant on scaled data in both groups. For the match group, the corresponding statistics were $F(3.1, 70.9) = 8.02$, $F(3.2, 74.6) = 10.34$, and $F(3.4, 77.9) = 6.60$ in each interval, respectively, all $p < .0001$. For the mismatch group, the statistics on scaled data in each interval were $F(4.2,$

Table 2. F Statistics and p Values of Key Effects in the Across-group ANOVAs on Electrical Brain Activity

Item Type	Effect	Latency Interval		
		100–700 msec	*700–1300 msec*	*1300–1900 msec*
	IT × GP × SM × ST	$F(3.6, 166.0) = 6.15$, $p < .0001$[a]	$F(4.3, 196.6) = 4.73$, $p = .001$	$F(4.1, 187.8) = 3.21$, $p = .014$
Words	GP × SM × ST	$F(3.8, 174.7) = 0.82$, $p = .508$	$F(3.6, 166.8) = 0.67$, $p = .600$	$F(4.3, 198.5) = 0.89$, $p = .476$
Pictures	GP × SM × ST	$F(3.7, 169.3) = 7.65$, $p < .0001$[a]	$F(4.1, 189.0) = 11.82$, $p < .0001$[a]	$F(4.2, 194.4) = 7.42$, $p < .0001$[a]

Degrees of freedom and p values are Greenhouse–Geisser corrected. GP = group; IT = item; SM = subsequent memory; ST = electrode site.

[a]Significant after scaling the data to remove overall amplitude differences between conditions (McCarthy & Wood, 1985).
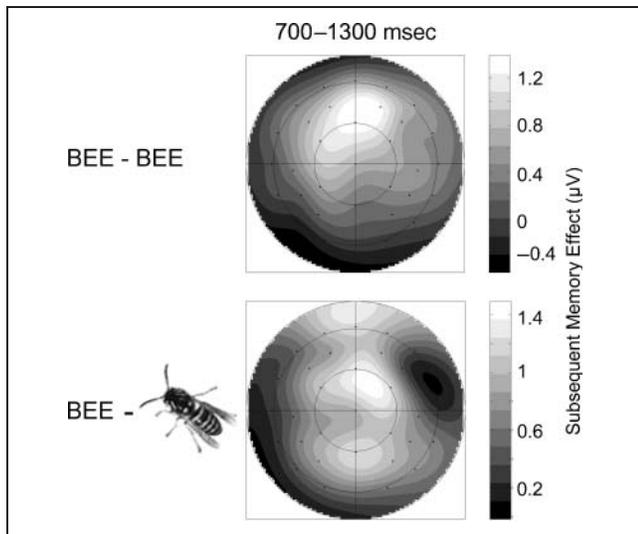
Figure 3. Scalp distributions of encoding-related activity for words. Two-dimensional voltage spline maps illustrating the distribution across the scalp of the ERP differences between later remembered and forgotten words in the 700–1300 msec latency interval following item onset. Maps are range scaled.

110.0) = 3.62, $F(4.3, 97.9) = 4.73$, and $F(4.5, 104.6) = 3.36$, all $p < .009$. Crucially, subsequent memory effects in the match group were significant over anterior but not posterior scalp sites. In contrast, effects in the mismatch group were significant over posterior but not anterior sites. Figure 4 shows the scalp distribution of the subsequent memory effects elicited by pictures in each group.

An interesting observation is that the qualitatively different subsequent memory effects for pictures seem mainly driven by ERPs elicited by items that were later forgotten (see Figure 2). Separate analyses on remember and forgotten pictures were conducted to substantiate this impression. No differences emerged in any latency interval when ERPs for remembered pictures were compared across groups ($ps > .288$). In contrast, the comparison of ERPs for forgotten pictures resulted in significant interactions between group and electrode site in the 700–1300 and 1300–1900 msec intervals, $F(2.9, 132.1) = 6.85$ and $F(3.8, 174.6) = 5.80$, respectively, both $p < .0001$.

DISCUSSION

We manipulated the similarity between study and test items to investigate how electrophysiological correlates of encoding vary depending on the degree to which functional processes engaged at study are engaged again at test. As expected, study–test congruency affected memory performance (e.g., Mulligan & Osborn, 2009; Mintzner & Snodgrass, 1999; Weldon & Roediger, 1987). The ability to discriminate old from new items was on the whole better when modes of presentation matched across study and test. The same pattern was observed when the analyses were restricted to items that were later recollected, although in this case the differences fell just short of statistical significance. The performance data thus generally support the idea that some aspects of memory are influenced by the interaction between processes at encoding and retrieval.

Table 3. F Statistics and p Values of the Key Effects in the Within-group ANOVAs on Picture-related Activity

		Latency Interval		
Group	Effect	100–700 msec	700–1300 msec	1300–1900 msec
Match	SM × ST	$F(3.1, 70.9) = 8.02$, $p < .0001$[a]	$F(3.2, 74.3) = 10.29$, $p < .0001$[a]	$F(3.4, 77.9) = 6.60$, $p < .0001$[a]
	SM anterior sites	$F(1, 23) = 15.37$, $p = .001$	$F(1, 23) = 26.06$, $p < .0001$	$F(1, 23) = 11.47$, $p = .003$
	SM posterior sites	$F(1, 23) = 0.21$, $p = .654$	$F(1, 23) = 2.70$, $p = .115$	$F(1, 23) = 0.05$, $p = .821$
Mismatch	SM × ST	$F(4.1, 93.7) = 3.34$, $p = .013$[a]	$F(4.5, 102.6) = 6.85$, $p < .0001$[a]	$F(4.5, 104.6) = 3.36$, $p = .009$[a]
	SM anterior sites	$F(1, 23) = 1.30$, $p = .267$	$F(1, 23) = 3.60$, $p = .071$	$F(1, 23) = 4.20$, $p = .052$
	SM posterior sites	$F(1, 23) = 12.45$, $p = .002$	$F(1, 23) = 31.14$, $p < .0001$	$F(1, 23) = 20.85$, $p < .0001$

Degrees of freedom and p values are Greenhouse–Geisser corrected. SM = subsequent memory; ST = electrode site. Anterior sites refer to the five most frontal electrodes in the montage (Sites 21, 34, 35, 36, and 50 of Montage 10 at www.easycap.de/easycap/e/electrodes/13_M10.htm). Posterior sites refer to five equivalent parietal ones (Sites 12, 14, 16, 26, and 29).

[a]Significant after scaling the data to remove overall amplitude differences between conditions (McCarthy & Wood, 1985).
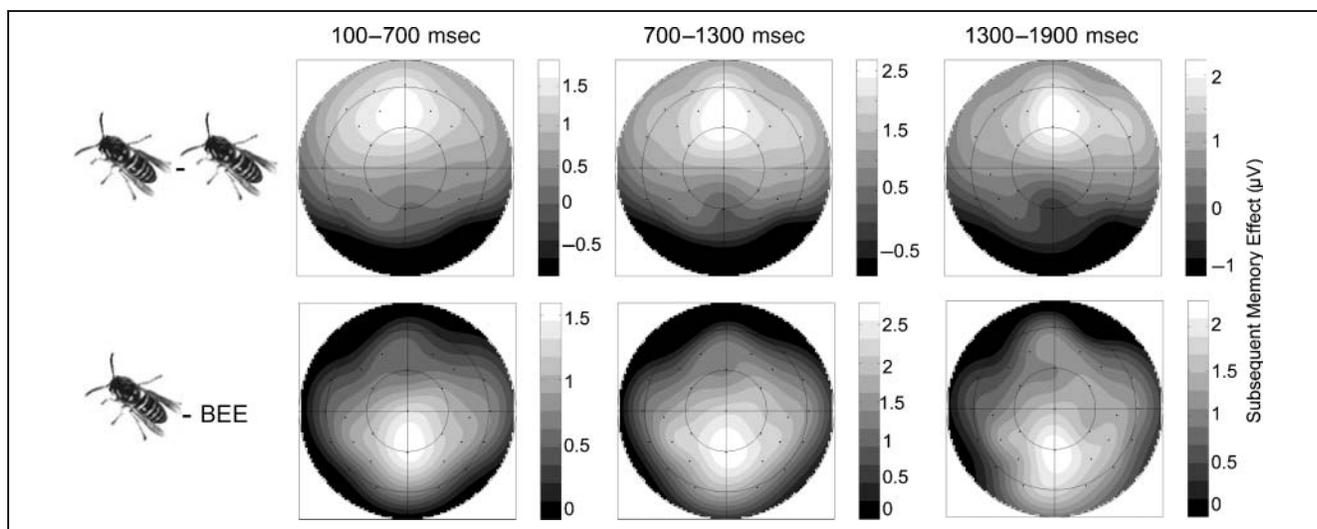
Figure 4. Scalp distributions of encoding-related activity for pictures. Two-dimensional voltage spline maps illustrating the distribution across the scalp of the ERP differences between later remembered and forgotten pictures in the 100–700, 700–1300, and 1300–1900 msec latency intervals following item onset. Maps are range scaled.

Study–test congruency had a profound effect on electrophysiological correlates of memory formation. Consistent with the transfer-appropriate processing framework (Roediger, 1990; Tulving & Thomson, 1973), different types of neural activity predicted encoding success when modes of presentation matched across study and test, relative to when they did not. However, this was only observed for one type of stimulus material. Although encoding-related activity for words did not differ depending on how memory was probed, pictures elicited activity with distinct scalp distributions from around 100 msec onward, depending on type of test cue.

These findings allow three main conclusions. First, they indicate that encoding-related brain activity can be affected by the interaction between processes engaged at encoding and retrieval. To our knowledge, this is the first demonstration that electrophysiological correlates of encoding differ qualitatively as a function of encoding–retrieval overlap. Second, encoding–retrieval overlap may play a direct, and not merely consequential, role in memory. This is because congruency in modes of presentation across study and test affected brain activity shortly after item onset. Third, the presence versus absence of an effect of study–test congruency for pictures and words, respectively, suggests that encoding–retrieval overlap is not a universal organizing principle of neural correlates of memory. Encoding-related activity not only seems determined by physical similarity across study and test but also by the degree to which functional processes overlap (cf. Roediger, 1990). Below, we discuss the implications in more detail.

The distinct subsequent memory effects observed in the present experiment corroborate previous suggestions that encoding-related activity varies depending on how memory is probed (Bridger & Wilding, 2010; Otten, 2007; Ranganath et al., 2004; Davachi et al., 2003). As

argued previously, activity seen with different retrieval cues must reflect separate aspects of an encoding episode. On any occasion, encoding-related activity reflects the processing of only those attributes that are used to later successfully retrieve an episode. If retrieval cues emphasize different attributes, encoding-related activity will differ accordingly. The present findings indicate that, in addition, encoding-related activity is affected by the degree to which attributes processed at encoding overlap with those processed at test. The attributes that are emphasized during encoding determine the nature of a representation in memory (Craik & Lockhart, 1972). Retrieval of a representation is more likely when the test cue emphasizes attributes that resemble those encoded into a representation (Craik, 2002). Brain activity that signals that an event will later be remembered will, therefore, highlight those attributes that overlap across study and test (Rugg et al., 2008; Otten, 2007). It will be of interest to determine, using a measure other than ERPs, whether the correspondence in the processing of attributes across study and test is accompanied by overlap in neural activity (cf. Norman & O'Reilly, 2003; Rolls, 2000; Alvarez & Squire, 1994).

The above explanation assumes that overlap in functional processes across study and test plays a direct, and not merely consequential, role in memory encoding. Unlike previous fMRI studies (e.g., Park & Rugg, 2008), the use of a technique with high temporal resolution allows the determination at what point in time effects of study–test congruency emerge. Direct effects are expected to emerge relatively early, shortly after the onset of an encoding event (Cameron et al., 2001). Effects that appear late are more likely to reflect processes downstream from encoding. The data indicate that study–test congruency affected encoding-related activity shortly

after item onset, at around 100 msec, persisting for at least 2 sec. This time course is consistent with a direct role of encoding–retrieval overlap in encoding.

In this respect, it is worth noting that the present findings do not fully mimic the results from Park and Rugg (2008). In that study, fMRI rather than EEG was used to assess whether encoding-related activity is sensitive to overlap in presentation modes across study and test. Unlike the material-specific effects observed in the present study, Park and Rugg (2008) found congruency effects for pictures and words. Electromagnetic and hemodynamic measures pick up different kinds of brain activity (Otten & Rugg, 2005) and different patterns of results may, therefore, be expected with each. There are also a number of design differences between the two experiments that compromise a direct comparison of the findings. These include reliance on remembered items versus the subsequent memory procedure, the use of an indoor/outdoor versus size judgment task, and the use of a within-subjects design versus between-subjects design. Nonetheless, the different patterns of results may highlight the limited temporal resolution of fMRI. It is possible that some fMRI activity presumed to be related to encoding is in fact related to processes downstream from encoding. This emphasizes the need to characterize encoding-related activity in time as well as space.

What are the crucial attributes that determine encoding-related activity on any occasion? The mere match or mismatch of presentation modes cannot control the identity of these attributes. No universal signature of match-related or mismatch-related processes was observed. Instead, encoding-related activity differed depending on the type of stimulus material. Regardless of how memory was probed, words that were later remembered elicited more positive-going ERPs over anterior scalp sites relative to words that were later forgotten. The scalp distribution of this modulation strongly resembles the subsequent memory effect typically observed in deep encoding tasks (Paller & Wagner, 2002; Friedman & Johnson, 2000). This effect is thought to reflect the degree to which an item's semantic and associative attributes are processed (Otten et al., 2007). On this account, words whose semantic attributes were processed more extensively during encoding were most likely to be remembered later on. It is not difficult to see why conceptual information helped retrieval of a word when the test cue was also a word. But, why would retrieval rely on conceptual information when the cue consisted of a picture? The answer to this question may lie in the use of mental imagery during the study task. Although the precise processes underlying size judgments are unknown, the objects denoted by study words may have been turned into mental images to help the decisions. Kosslyn (1975) demonstrated that size judgments involve mental imagery and all participants in the present experiment reported the use of an imagery strategy during debriefing. The perceptual details of images created at study could have formed the basis of retrieval. However,

overlap in perceptual information will have been limited because internally generated images are physically distinct from the images actually presented at test (Nelson, Reed, & McEvoy, 1977). The best strategy to retrieve words with picture cues may, therefore, have been to rely on the overlap in conceptual attributes.

For pictures, encoding-related activity differed depending on type of retrieval cue. When pictures were probed with pictures, activity over anterior scalp sites predicted encoding success. When pictures were probed with words, activity was instead maximal over posterior sites. The scalp distribution differences imply that qualitatively distinct processes underlie effective encoding in each case (Otten & Rugg, 2005). Previous studies using pictures at both study and test also found anterior subsequent memory effects (Aiqing, Chunyan, Yanhong, Nan, & Jinhong, 2004; Duarte, Ranganath, Winward, Hayward, & Knight, 2004). Given the functional role of anterior effects (Otten et al., 2007), successful encoding must have entailed the processing of a picture's semantic attributes when the test probe also consisted of a picture. Overlap in conceptual processes may have been easier to rely on than overlap in perceptual processes given the complexity involved in the latter. However, the early onset and large size of the effect in the present experiment suggest that perceptual attributes may play at least some role.

Intuitively, one might have expected similar—conceptual—encoding processes in the "picture–word" as in the "word–picture" condition because both involve a perceptual mismatch. However, the determination as to whether an item occurred earlier may have required inspection of the perceptual details of a stored representation only in the "picture–word" condition. When faced with a word cue at test, a mental image of the object may have been created in an attempt to match the cue with a picture encountered at study. A decision about the previous occurrence of an item required the recovery of perceptual details to ensure that it was that particular item—and not one that resembles it—that was previously encountered. On this account, pictures whose perceptual attributes were processed more extensively at study were those which were most likely to be remembered with word cues. Previous work has indeed linked posterior subsequent memory effects to visualization (Gonsalves & Paller, 2000) and the processing of specific stimulus attributes (Otten & Donchin, 2000; Fernandez et al., 1998; Fabiani, Karis, & Donchin, 1986; Karis, Fabiani, & Donchin, 1984).

The qualitatively different subsequent memory effects for pictures primarily arose because of differences in forgotten pictures. This does not shed more light on the functional interpretation of the observed effects. However, it raises the intriguing possibility that it is not the engagement of encoding-relevant activity that aids encoding but the lack of engaging such activity that hampers it. This is a subtle, but possibly important, difference.

Regardless of the validity of the above interpretations, the present findings clearly indicate that study–test congruency plays a role in encoding-related brain activity. The selective influence of congruency on pictorial stimulus material suggests that it is not only the physical similarity between study and test items that influences encoding-related activity but also the degree to which functional processes overlap (cf. Roediger, 1990). Pictures usually involve the processing of conceptual as well as perceptual attributes, whereas words tend to be restricted to the processing of conceptual attributes (McBride & Dosher, 2002; Mintzner & Snodgrass, 1999; Nelson et al., 1977). The more attributes an event possesses, the more likely it is that the use of attributes varies across study and test. Transfer-appropriate processing effects in memory performance are indeed more prevalent for pictorial information (Reingold, 2002; Rajaram, 1993; Weldon & Roediger, 1987). The use of grayscale photographs of everyday objects in the present experiment may have further enhanced the number of attributes that are processed. An interesting direction for future research is to manipulate the type and number of attributes that need to be encoded and retrieved within and across stimulus classes (Nyhus & Curran, 2009).

A final comment concerns the fact that we restricted the analyses to study items later given remember judgments. Because of this, the effects of study–test overlap cannot easily be attributed to differences in type of recognition judgments. It is not clear from the present data, however, what type of judgment is especially sensitive to encoding–retrieval overlap. Items later given know judgments could not be analyzed in isolation and remember judgments have been attributed to recollection (Yonelinas, 2002; Tulving, 1985) or especially strong memories (Wais et al., 2008). Previous studies on the impact of encoding–retrieval overlap on neural measures only considered old/new judgments (e.g., Park & Rugg, 2008; Schloerscheidt & Rugg, 2004) and behavioral studies contrasting different sources of recognition show inconsistent results. Whereas some studies report that perceptual congruency only affects recollection (Reder, Donavos, & Erickson, 2002; Hirshman, Passanante, & Arndt, 1999), others report effects specific to familiarity (Jacoby, 1996), and yet others effects for both recollection and familiarity (Rajaram, 1993). It, therefore, remains an open question whether study–test congruency affects recollection, familiarity, or both.

In conclusion, we have demonstrated that electrophysiological correlates of memory formation are sensitive to the interaction between encoding and retrieval (cf. Roediger, 1990; Tulving & Thomson, 1973). Encoding–retrieval overlap may play a direct role in encoding given its time course and can affect the encoding of some but not all stimulus materials. Importantly, the findings not only add to our theoretical knowledge of the neural bases of long-term memory but also have practical implications. The demonstration that encoding–retrieval overlap affects neural correlates of encoding dictates caution when interpreting differences in encoding-related activity observed across groups or conditions. Such differences do not necessarily reflect different encoding operations but may instead reflect encoding–retrieval interactions.

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