

EPISODIC MEMORY, INTEGRATIVE PROCESSING, AND MEMORY-
CONTINGENT BRAIN ACTIVITY DURING ENCODING

By

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EPISODIC MEMORY, INTEGRATIVE PROCESSING AND MEMORY-
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A fundamental element of encoding an experience is establishing a link between an object or event and its spatiotemporal context. Current theories posit important roles for the prefrontal cortex and medial temporal lobe complex in successful episodic “binding.” We conducted two experiments to isolate the timing and scalp topography of event-context encoding effects using event-related brain potentials (ERPs). Participants were shown sequential (3 sec. apart) word pairs (e.g., ELEPHANT . . . BATHROOM) while their electroencephalograms (EEG) were recorded. Some participants were instructed to generate a single, integrated mental image while other participants generated a pair of separate images. Their ability to recognize intact pairs was then tested. As expected, recognition was better for pairs studied under Bound than under Separate instructions. ERP encoding differences between later recognized pairs and later forgotten pairs (**D**ifferences associated with subsequent **m**emory performance or “*Dm*”), especially at frontal sites, were found for the Bound, but not the Separate, condition. These slow-

wave differences were seen late following both words; however, the differences were of opposite polarities and contrasting morphology. An early, first-word difference between the waveforms for intact pairs that were subsequently recognized in the Bound versus the Separate conditions suggested different preparatory sets in the two tasks. In the second experiment, participants were given the same imagery tasks but tested subsequently for item, rather than pair, recognition. Unlike the first experiment, participants showed no difference in recognition performance by image generation task. As in the first experiment, there were ERP differences for correctly recognized vs. unrecognized items in the Bound condition, but these item-specific Dm's were earlier and of a different topographic distribution than the Dm's for pair recognition. No Dm effects were noted for the Separate condition. The contrasting ERPs between the Separate and Bound conditions, and the contrasting Dm's for ERPs conditionalized on item versus pair recognition, suggest that relational processing contributing to successful object-location memory requires effortful processing, and is associated with frontal or prefrontal regions of the cortex.

CHAPTER 1 INTRODUCTION

This dissertation presents a pair of experiments that explore the cognitive and neural bases of episodic memory encoding. In particular, the studies examine the creation of a mental link between events and their spatiotemporal contexts by recording event-related brain potentials (ERPs) and conditionalizing those electrophysiological measures on subsequent memory performance in different tasks and under different instructions.

Events, Context, and Episodic Memory

As Tulving (1984) has noted, the basic unit of an individual's perception of time is an "event;" that is, some occurrence at a given place at a given time. An ongoing series of events make up an "episode." Episodic memory enables humans to "time travel;" that is, to place ourselves in the recent or distant past, or even, the imagined future (Tulving, 1985). Without episodic memory, one lives in a constant, immediate present, like the well-known amnesic musician, Clive Wearing. Successful episodic memory performance, therefore, requires that the episode's context be linked with the focal event itself upon its initial occurrence. It is this linkage of spatiotemporal context and focal event that enables us to separate personally experienced, geographically distinct, but close in time, events from one another ("First I was in the kitchen, then I went into the dining room"). Moreover, we use episodic memory to distinguish identical or similar events by the order of their temporal occurrence ("I saw a dog run across the street yesterday. I saw the same dog run across the street this morning").

As important as this spatiotemporal linking of event and context is for memory, it apparently is not an obligatory or automatic one; indeed, one of the classic “sins of memory” (Schacter, 2001) is to remember an event but forget the context, or remember it falsely in the wrong context. A wide variety of experimental protocols have shown that both healthy participants (Chalfonte & Johnson, 1996; Henkel, Johnson, & DeLeonardis, 1998; Mitchell, Johnson, Raye, Mather, & D'Esposito, 2000; Mitchell, Johnson, Raye, & D'Esposito, 2000) as well as neurologically impaired patients (Turriziani, Fadda, Caltagirone, & Carlesimo, 2004) can retain relatively good levels of item recognition yet show substantial decrements in the ability to identify either the spatiotemporal context in which a recognized item was presented or to recognize (an) additional feature(s) with which the to-be remembered item was to be associated. Thus, the processes that support item recognition or recall appear to be distinguishable from those that support contextual memory.

A widely held analogy has been drawn between the ability to remember the contextual features of an event, and the subjective sense of remembering that has been termed “recollection.” Indeed, since the mid-1980’s, the qualitative distinction between “remembering” and “knowing” (Tulving, 1985) (or “recollection” versus “familiarity” for others) has been a central topic in the study of episodic memory (e.g., Yonelinas, 2002). The precise natures of the processes that support recollection are still largely undefined. It is clear that sensory information must be transformed into internal representations. However, to permit successful subsequent recollection, the elements of sensory experience, together with any relevant internally generated cognition and emotional

states, must be combined in such a way that the experience is capable of later being reinstated (Paller & Wagner, 2002).

Understanding the cognitive and neural processes that support successful episodic memory performance involves analyzing events both at encoding and at time of retrieval. While there has been a significant amount of research examining the retrieval-associated processes in episodic memory, far fewer studies have pursued the encoding processes that underlie episodic memory formation. For example, the degree to which, and conditions under which, attention plays a role in the encoding of context is unknown. Given the continuous stream of information one encounters, it seems likely that some degree of automaticity is required for everyday episodic memory to function efficiently. However, while Hasher and Zacks (1979) suggested that fundamental information such as time, spatial location and frequency of occurrence may be encoded relatively automatically, Craik (1989) suggested that, in some cases, attention might play an important role in the integration of an event with its context.

Furthermore, the content and the context may interact to make the context more memorable (e.g., an elephant on the sidewalk is more memorable than a jogger on the sidewalk but a jogger in the zoo may be as memorable as an elephant in the zoo). Finally, it is unclear whether locations and their associated objects are bound together (and subsequently retrieved) in a single representation in holistic fashion, or if a link or pointer is formed that connects independently created and maintained episodic representations.

The experiments presented in this dissertation are an attempt to identify some of the neural and cognitive encoding processes that support successful item + context

retrieval and distinguish them from the encoding processes that support successful item-only retrieval.

Creating Episodic Memories: Theories and Data

Long-term memory research has identified a variety of encoding factors (e.g., organization among items in a list; “depth” or degree of elaborative item processing, item frequency or familiarity) that are associated with successful long-term memory. The processes by which items or events and their contexts are bound, however, have been little explored. While traditional principles of associative learning (e.g., intra- and extra-item organization) may apply, it is possible (or even likely) that other discoverable, Gestalt-like principles may be at work (Craik, 1989; Kounios, Smith, Yang, Bachman, & D'Esposito, 2001).

In a series of unpublished studies, Craik (1989) explored the effects of stimulus integrability and attention on the degree to which item and context recall were independent. Overall, he found that context recall declined more rapidly initially than item recognition as attention was diverted during study, but, as context recall approached chance levels, item recognition then dropped quite rapidly. Moreover, for items and contexts that were thought to be more “integrable,” memory performance for items and contexts were more closely bound to one another. An important, yet unanswered question is what factors might affect integration of item and context. Craik suggested that the emotional content of the item-context could affect the ease of integration. Nevertheless, there has been little work, to date, on the cognitive and neural processes that successfully link events to their contexts in long-term memory.

Three areas of research, reviewed below, may provide some guidance. First, a few working memory studies (Chalfonte & Johnson, 1996; Luck & Vogel, 1997; Mitchell et

al., 2000a; Mitchell et al., 2000b; Prabhakaran, Narayanan, Zhao, & Gabrieli, 2000; cf., Bor, Duncan, Wiseman, & Owen, 2003) have examined the binding of an object and other feature information (e.g., spatial location, color) in working memory. If the processes engaged during working memory binding are utilized in long-term memory encoding, these studies are important in revealing the basis of episodic encoding. Second, use of physiological measures of brain activity such as electroencephalographic (EEG) recording to identify event-related brain potentials (ERPs) have revealed cognitive and neural processes that differentiate successful and unsuccessful long-term memory encoding. Third, event-related functional magnetic resonance imaging (ER-fMRI) studies have begun to reveal subcortical regions and areas in medial temporal (MTL) and prefrontal (PFC) cortex that distinguish successful and unsuccessful long-term memory encoding. Each of these areas of research will be discussed below.

Working Memory Studies of Object-Location Binding

In a number of studies, participants were required to briefly maintain two or more stimulus features or dimensions either separately, or in an integrated representation. These studies have shown that the ability to remember an object-location association is distinguishable from the ability to remember objects or features separately. Thus, for example, the deficits that older adults show in source memory cannot be attributed merely to the inability to remember a greater number of objects or features (Chalfonte & Johnson, 1996; Mitchell et al., 2000a; Mitchell et al., 2000b). The processes that underlie the short-term maintenance and manipulation of objects in working memory have been characterized as “reflective processes” (Johnson, 1992), but it is unclear whether these processes play a role in successful long-term memory for object and context binding. It is unclear, also, whether working memory and long-term memory encoding share a set of

common cognitive processes. If so, these working memory studies may reveal some of the principles at work in successful episodic binding.

Recently, there has been some convergence on this issue (Baddeley, 2000; Fletcher & Henson, 2001; Johnson, 1992; Wagner, 1999). Some investigators have claimed that working memory and long-term memory encoding share a common set of processes (Wagner, 1999) while others (Baddeley, 2000) have proposed common structural components between working memory and long-term memory.

According to one view (Baddeley, 2000), binding of information from verbal and non-verbal slave systems takes place in an “episodic buffer” that stores that information in a multimodal code or representation. This bound information can then be passed back and forth between working memory and long-term “episodic” memory. According to this view, working memory and long-term episodic memory share an interlocking component (the episodic buffer) and a set of common processes (binding and maintenance in the buffer). An alternative view is one that emphasizes the commonality of the cognitive processes that underlie working memory and long-term memory performance (e.g., Fletcher & Henson, 2001; Johnson, 1992; Wagner, 1999) . In its most developed form, this approach is process-specific (versus task-specific) and its goal is to identify and define the processes that underlie a variety of mnemonic and other cognitive phenomena.

The most developed example of this type of model is Johnson’s (1992; Johnson & Hirst, 1993) multiple-entry, modular memory (MEM) framework. It presupposes that a common set of cognitive subprocesses act on a variety of cognitive tasks. Thus, according to the model, the subprocesses used in working memory binding operate in successful long-term episodic encoding as well. The MEM model includes high-level

subprocesses such as initiating plans; discovering relations among stimuli; rehearsing and retrieving and lower-level subprocesses such as noting relations; shifting attention; refreshing currently active representations and reactivating stored representations.

Johnson and colleagues' work has examined the nature of the object-location binding deficits observed in older (relative to younger) adults (Chalfonte & Johnson, 1996; Mitchell et al., 2000a; Mitchell et al., 2000b). In various studies (Mitchell et al., 2000a; Mitchell et al., 2000b; Ranganath, Johnson, & D'Esposito, 2003; Raye, Johnson, Mitchell, Reeder, & Greene, 2002), she and her colleagues have suggested that deficits in feature binding may be attributable to difficulties in reactivating stored representations and in failing to refresh currently active representations. Although Johnson and colleagues' studies provide evidence of a set of cognitive subprocesses that are involved in binding object and location features in working memory, their findings have not been extended to long-term memory encoding.

In a recent study using event-related functional imaging, or fMRI (see following), however, Ranganath and colleagues (2003) have compared the areas of neural activation associated with working memory and successful long-term memory encoding. They found that separate face-encoding tasks, with identical stimuli but different encoding loads and retention intervals, activated similar areas of prefrontal cortex. While this finding suggests that the same cognitive (or at least neural) processes underlie certain working memory tasks and long-term memory encoding, methodological and experimental constraints make such conclusions tentative at best.

Thus, a few studies (Chalfonte & Johnson, 1996; Luck & Vogel, 1997; Mitchell et al., 2000a; Mitchell et al., 2000b; Prabhakaran et al., 2000) have considered the issue of

how working memory binds separate stimulus dimensions or features into an integrated whole. To date, however, there has been, to my knowledge, no direct measurement of long-term memory performance following the systematic manipulation of stimulus features, dimensions or combinations of stimuli to promote or inhibit working memory binding. A relatively direct way to study the neural and cognitive bases of long-term memory encoding is to record some physiological index of cognitive activity during an encoding event and then sort those records by subsequent memory performance during a later memory test. Such procedures have yielded reliable differences between later-remembered and later-forgotten items using both EEG and fMRI measures. Functional MRI studies suggest that these subsequent memory effects are associated with heightened medial temporal lobe (MTL) and prefrontal cortex (PFC) activation. However, the precise role of these structures in long-term memory encoding is still unclear. Findings from EEG studies, while isolating subsequent memory differences from about 400 ms onward following stimulus presentation, have varied substantially from one another both in the locus and timing of subsequent memory effects. As a result, EEG subsequent-memory studies have done little to identify the important processes that link event and context in memory encoding.

ERPs and Episodic Encoding

The use of stimulus-locked, event-related brain potentials has been a valuable tool in identifying a variety of neurocognitive memory processes over the past two decades. For example, a robust finding is that correctly recognized old items show a greater positivity than correctly identified new items. These “Old-New” effects have been shown with a large variety of stimulus materials in many test formats. A less robust, but well-replicated, finding is that, under certain circumstances, studied stimulus materials that

will be subsequently recognized as “Old” show a greater positivity than items that will later be classified erroneously as “New.” These subsequent memory effects (or “Dm” - Differences associated with subsequent memory performance) have been used to examine encoding in long-term memory.

The Dm/subsequent memory effect

Most ERP studies of encoding have used the same basic paradigm. In this paradigm, electrical activity is recorded while subjects are presented with stimuli that are subsequently tested under either explicit (e.g., recognition, cued recall) or implicit (e.g., stem-completion) conditions. These records are then classified according to subsequent memory (recalled/recognized vs. unrecalled/unrecognized) performance. Quite a number of investigators (Besson & Kutas, 1993; Duarte, Ranganath, Winward, Hayward, & Knight, 2004; Fabiani & Donchin, 1995; Fabiani, Karis, & Donchin, 1986; Fernandez et al., 1999; Fernandez et al., 1998; Friedman, 1990; Friedman, Ritter, & Snodgrass, 1996; Friedman & Trott, 2000; Gonsalves & Paller, 2000; Guo, Voss, & Paller, 2005; Guo, Zhu, Ding, Fan & Paller, 2004; Karis, Fabiani, & Donchin, 1984; Lian, Goldstein, Donchin, & He, 2002; Mangels, Picton & Craik, 2001; Mecklinger & Muller, 1996; Munte, Heinze, Scholz, & Kunkel, 1988; Neville, Kutas, Chesney, & Schmidt, 1986; Sanquist, Rohrbaugh, Syndulko & Lindsley, 1980; Schott, Richardson-Klavehn, Heinze, & Duzel, 2002; Smith, 1993; Summerfield & Mangels, 2005; Van Petten & Senkfor, 1996; Weyerts, Tendolkar, Smid, & Heinze, 1997; Yovel & Paller, 2004) have shown differential scalp recorded electrical activity at encoding between subsequently remembered and unremembered stimuli (“difference associated with memory” (Dm) or “subsequent memory effects”). These differences usually, but not always, consist of a greater positivity for remembered items than for unremembered items, although the

timing and topography of these effects vary depending upon the precise experimental conditions. Some published studies report the effects as containing a frontal maximum. Others show robust midline effects; and yet other studies have a posterior maximum (Johnson, 1995; Rugg & Allan, 2000). Some portion of this variance may be due to the difference in stimulus materials across studies (Johnson, 1995).

Dm and associative encoding

Only a handful of published studies (Guo et al., 2005; Fernandez et al., 1998; Kounios et al., 2001; Weyerts et al., 1997; Yovel & Paller, 2004) have sorted encoding ERPs for associative information by memorial success. Kounios and colleagues (2001) isolated electrical activity associated with faster (better) subsequent memory for associated words than for more slowly recognized associated words. They explored whether two proposed processes of cognitive association, juxtaposition and fusion, have different neural bases. They presented word pairs that either could be fused to create a novel concept (e.g., *computer-virus*) or could not easily be combined into a single unique concept (e.g., *salt-pepper*). Using a dense electrode array, they measured electrocortical activity as participants decided whether or not fusion was possible. Subsequently, pairs were re-presented, one half in the same order (e.g., salt-pepper), one half reordered (e.g., virus-computer). Participants judged whether the pairs were as presented previously or reordered. Faster word pair order judgments were deemed to represent better memory (and hence better encoding). A median split of the word pair order judgment RTs showed that fusible pairs that were judged fusible more quickly at study were also responded to more quickly at test. Conversely, non-fusible (juxtaposed) pairs to which participants responded more quickly at study were responded to more slowly at test.

As with the behavioral data, ERP data were classified by response speed at test. Both juxtaposed and fusion pairs showed an effect at study of the speed of the responses at test. This “subsequent memory effect,” however, is different from the standard subsequent memory effects discussed above. First, it is important to emphasize that the ERP memory differences are between (ostensibly) better and more poorly remembered word pair orders, not between remembered and unremembered items. Second, although the fused pairs showed a greater positivity for faster than for slower judgments, the juxtaposition pairs showed the opposite pattern, with slower word order judgments being associated with a greater positivity than faster judgments. These retrieval speed effects persisted throughout the recording epoch. Kounios and colleagues interpreted the ERP retrieval differences and the subsequent localization of those differences to the right prefrontal cortex as indexing processes associated with an attempt to fuse the words of the pair. Such processes might include maintenance of the pair in working memory, construction of candidate fusions, and evaluation of these fusions. Implementation of such processes would explain why the ERP effects would be present in the early epoch (200 – 800 ms) of both fusion and juxtaposition pairs, but would persist into the middle epoch (800 – 2100 ms) only for juxtaposition pairs – in which the search for an appropriate fusion might be expected to continue.

Weyerts and colleagues (1997) examined the ERP correlates of two semantic encoding tasks. One task required determining whether either word of a pair was associated with a given color; thus the task demanded semantic evaluation of both words, but the associative relationship between the pair was irrelevant (nonassociative task). The second task required participants to judge whether the words of the pair were

semantically related to one another. Again, semantic analysis was required of each word of the pair, but the task further required participants to judge the items' interrelatedness (associative task). Old and new word pairs were presented in a subsequent incidental recognition memory test. Subsequent memory effects for words encoded in the associative tasks were found at frontal sites, with right frontal effects greater than left frontal effects. No subsequent memory effects were found for the nonassociative encoding task. The authors interpreted the difference in subsequent memory effects between the associative and nonassociative tasks as reflecting the creation of a more elaborated memory trace in the associative task than in the nonassociative task.

Dm and elaborative encoding

Another group of studies (Duarte et al., 2004; Fernandez et al., 1998; Friedman & Trott, 2000; Guo et al., 2004; Mangels et al., 2001; Schott et al., 2002; Smith, 1993) has observed subsequent memory effects that appear to be associated with elaborative processing (when the task does not explicitly demand that participants process stimuli relationally). For example, Mangels, Picton and Craik (2001) had participants memorize lists of 45 words for subsequent explicit recall and recognition tests. The words were studied under either full attention or divided-attention (*not discussed*). Participants were given no particular instructions for memorizing the words. At test, participants first were given three minutes to recall as many of the words as possible. Thereafter, they were shown a series of words (50% old) to which they responded, "remember," "know," or "new" (following the Remember-Know paradigm of Tulving, 1985). Subsequent memory effects showed both an anterior positive and a posterior negative sustained potential. Mangels and colleagues pointed out that the sustained anterior positivity was consistent with a few earlier findings in which late, sustained anterior subsequent memory effects

were induced when the study task involved biasing participants toward the elaboration of the stimuli. They pointed out that it was unclear which types of elaborative processes were involved in their task. They speculated, however, that the anterior positivity may have consisted of two separate components: (1) an earlier, left-sided positivity representing activation of processes involved in associational or relational processing between the stimulus and information in semantic memory and (2) a later, more right-sided effect representing retrieval of previous list items no longer in current awareness and comparison processes necessary for strategic organization of list items. Despite their speculation, the task used by the investigators did not explicitly manipulate any of these purported processes; so further evidence is necessary to confirm their claims.

Mangels and colleagues attributed the sustained posterior negativity to the representation of the concrete object represented by the word or the representation of the word itself. They pointed out, however, that such posterior inferior sustained negativity had been identified in only one other study. They attributed this lack of similar findings in the subsequent memory literature to their choice of using an average, rather than a mastoid or earlobe, reference. They pointed out a similar negativity at the mastoid electrodes (TP9/10) which would have been subtracted out had they been used as a reference.

Mangels and colleagues also identified a parietal positivity (P280) and a fronto-temporal negativity (N340) that separated old words that were subsequently missed from recognized words (but which did not distinguish between R and K items). They concluded that processing up to about 340 ms consisted of the perceptual analysis and selection of the item as task relevant followed by item-specific semantic processing

(N340). Once this processing is completed, the information is made available to the MTL system for long-term storage (P550). Thereafter, relational and elaborative processing takes place via the sustained interaction between frontal and inferior temporal regions beginning at about 1000 ms.

In an aging study (Friedman & Trott, 2000), participants studied sentences containing two unrelated nouns (e.g., “The dragon sniffed the fudge.”) for a subsequent explicit recognition test. At test, participants made “Old/New” recognition judgments, followed by “Remember/Know” decisions to items judged “old.” Finally, participants made temporal order decisions (List 1 vs. List 2). Study ERPs, sorted by recognition decision, showed a widespread Dm effect among young participants for Remember decisions only but for both Remember and Know decisions in the older participants. Friedman and Trott proposed that encoding of items by older participants was less contextually rich, even for old items judged “Remember,” than encoding of “Remember” items by younger participants. Alternatively (or in conjunction with this shallower encoding proposal), Friedman and Trott suggested that older participants might have applied a more liberal criterion to the Remember/Know judgments than did the younger participants. Moreover, they pointed out that, unexpectedly, there was no correspondence between Dm effects associated with Remember/Know judgments and source list judgments. They noted that Remember judgments could be assigned if *any* aspect of the encoding session was retrieved, regardless of whether the list from which the item was taken was retrieved. Thus, Remember responses may or may not have been accompanied by correct source list judgments.

Therefore, although Friedman and Trott used a nominally associative encoding task in which participants were given two unrelated words within a sentence, neither the test (identification of each word as old or new), nor the instructions (“memorize the nouns for a subsequent memory test) explicitly demanded that the words be encoded together. In fact, at test, rearranged old items required “Old/Old” responses. Thus, encoding the items as a pair could make it more difficult to respond “old” to the second word if it were repaired. Therefore, Friedman and Trott showed a widespread Dm effect that varied by the response type (Remember/Know) and interacted with age. The study does not, however, clarify the nature of the encoding at study that produced the Dm although their suggestions that lack of differences between Remember and Know responses for older participants reflected shallower encoding, or less elaborated traces, is attractive.

A recent study, however, suggests that ERP effects produced by a levels-of-processing (LOP) manipulation differ in onset, duration, and topography from ERP Dm effects. Schott and colleagues (2002) found an LOP effect (deep > shallow) at fronto-central regions that began at about 600 ms after stimulus onset and lasted until the end of the recording interval. This contrasted with widespread Dm effects from 600 - 800 ms that were associated with only the shallow encoding condition and a right frontal Dm from 900 – 1200 ms associated with both study conditions. Schott and colleagues argued that the LOP effects might represent differences in retrieval from semantic memory required by the two tasks whereas the Dm effects might represent the establishment of an episodic memory trace. They disagreed with Van Petten and Senkfor’s (1996) conclusion that Dm effects for meaningful words, but not for meaningless, novel visual patterns,

suggests that the Dm reflects retrieval from semantic memory and point out that Van Petten and Senkfor's "Dm" effects might have consisted of both differences in study processing and in establishment of the memory trace. Schott and colleagues argued further that the early and late Dm effects (which were modulated by LOP) likely reflect different processes. For example, the early, widespread Dm (which was present only for words studied in the shallow condition) might have been associated with the formation of memory traces containing distinctive orthographic/phonological information. On the other hand, the late, right prefrontal Dm, which occurred with both study conditions, might signify the establishment of a memory trace with semantic-associative information. They argue that occurrence of this Dm in the shallow study condition might simply reflect the activation of semantic-associative information during the shallow study task and note that a similar Dm was found during a rote rehearsal task by Fernandez and colleagues (1998).

Finally, Fernandez and colleagues (1998) interpreted the existing subsequent-memory-effect literature as consisting of two effects: a centroparietal effect associated with rote encoding strategies, regardless of distinctiveness, and a frontal effect that is associated with elaborative encoding (Fabiani, Karis & Donchin, 1990; Karis, Fabiani & Donchin, 1984; Weyerts et al., 1997). In their own study, they examined the differences in encoding ERPs associated with item distinctiveness, associative elaboration, or other "direct" encoding processes. They presented 40, 15-item, word lists, consisting of high and very low frequency words. Each list was followed by a brief distraction period and a free recall task. One half of the lists were blocked by word frequency and one half of the lists contained both high and very low frequency words. Fernandez and colleagues

assumed that associative (inter-item) encoding would facilitate recall of the high- versus low-frequency words in the blocked lists, and yield intermediate (relative to low-frequency/mixed and high frequency/blocked) recall rates in the mixed lists. Moreover, they assumed, consistent with Karis, Fabiani & Donchin (1984), that the amplitude of the N400 and P300 (LPC) would be associated with distinctiveness and thus should be associated with low-frequency, more than high-frequency, words. Any subsequent memory effects unrelated to distinctiveness detection should be dissociable in topography, amplitude, and/or time course from the enhanced N400/LPC. Moreover, a subsequent memory effect that was greater for high- than for low-frequency words, and enhanced further in the blocked condition, would be likely to correspond to associative processing. If the subsequent memory effect did not interact with word frequency and presentation (blocked/mixed), then it would be likely to be related to nonassociative encoding processes.

Subsequent memory effects were dissociable into separable components. One effect arose at centroparietal and frontopolar sites at about 200 ms for high-frequency words and at about 350 ms for low-frequency words. It shifted to a single frontopolar maximum at about 900 ms that differed both in topography and time course from the distinctiveness effects associated with word frequency. A second subsequent memory effect, located at a right frontopolar site at between 900 and 1300 ms, occurred for high-, but not low-, frequency words. Fernandez and colleagues concluded that they had identified subsequent memory effects that were associated neither with distinctiveness nor with associative processing. Although the second effect was located at right frontobasal electrodes, as predicted, it was associated only with successfully recalled

high-frequency words. Further inspection showed that only unsuccessfully recalled high-frequency words failed to elicit any effect at this site; all other types (high-frequency, successfully recalled and low-frequency, successfully and unsuccessfully recalled) showed greater amplitude at the frontobasal sites. However, there was no interaction with presentation type.

ERP summary

A modest number of studies have examined the ERP correlates of encoding. A few have compared study phase data across encoding manipulations (e.g., levels of processing). Numerous methodological difficulties arise with such comparisons (e.g., equating memorial success across tasks) but it appears that “deep” encoding (relative to shallow encoding) yields a long-lasting, centroparietal positivity that onsets about 600 ms after stimulus presentation. The observed ERP differences might reflect retrieval from semantic memory required in “deep” encoding, but such conclusions are mostly speculative. A second group of ERP encoding studies have compared the ERP correlates of successfully recognized (or recalled) items with old items that are unsuccessfully recognized (or recalled). These subsequent memory effects (or differences associated with memory - “Dm”) have been produced using both recognition and recall tests across a wide variety of experimental conditions. Although some commentators have found it difficult to generalize from the disparate subsequent memory effect findings, it appears that hypotheses regarding the nature of the processes underlying the later subsequent memory effects may be tested. For example, Schott and colleagues have speculated that the late, right frontal Dm observed in their study, as well as in others’ studies, may signify the formation of memory traces containing semantic associative information.

Nevertheless, the essence of episodic memory is that it includes both the item and the item's context. Although some ERP studies have purported to examine memory for "context" or "source" memory, these studies have largely only had participants associate a single perceptual attribute (e.g., voice, temporal order, spatial location). Moreover, the nature of such experiments is to repeat a non-meaningful attribute across items, rather than having participants encounter each item in a unique context, which is likely to support retrieval differently than when the context (or perceptual attribute) does not possess unique characteristics.

A few published event-related potential (ERP) studies (Duarte et al., 2004; Friedman & Trott, 2000; Guo et al., 2005; Kounios et al., 2001; Mangels et al., 2001; Smith, 1993; Schott et al., 2002; Weyerts et al., 1997; Yovel & Paller, 2004) have examined context-event or associative encoding. Some of those studies have used the "Remember-Know" paradigm to distinguish subsequent memory with context recognition from subsequent memory without context recognition. The findings across these studies are inconsistent. For example, Smith (1993) found that the subsequent memory effects (Dm) were similar in timing and topography, regardless of whether they were associated with "R" or "K" responses. On the other hand, Friedman and Trott, (2000) found significant Dm effects for subsequent "R," but not "K," responses in young participants. However, older participants showed Dm effects to both "R" & "K" responses. Unlike Smith, however, Friedman and Trott found that the Dm effect was lateralized ($L > R$), in the young participants (although not in the older participants).

In contrast to the findings of both Smith (1993) and Friedman and Trott (2000), Duarte and her colleagues (2004) found transient, left frontal Dm effects for items later

classified as “K” and sustained, bilateral (with right > left) Dm effects for items later classified as “R.” Similarly, Mangels, Picton & Craik (2001) found left-lateralized, fronto-temporal subsequent memory effects at N340 for both R and K responses, which didn’t differ from one another. The differences across these studies are difficult to reconcile.

Of the remaining studies, two (Guo et al., 2005; Yovel & Paller, 2004) involved the encoding of novel faces with associated information (names, occupations). Although Dm effects were observed for encoding of face-name and face-occupation associations, these effects were neither lateralized, nor transient. Rather, they were long lasting and topographically central or centro-posterior.

Functional Imaging and Associative Encoding

A large number of functional MRI and PET studies have examined neural activity at encoding (see Cabeza & Nyberg, 2000; Fletcher & Henson, 2001; Fletcher, Frith, & Rugg, 1997; Mayes & Montaldi, 1999; Nyberg, 2002; Schacter & Wagner, 1999 for reviews). The development of event-related fMRI enabled investigators to sort these encoding records by subsequent memory performance. Since then, a large number of studies (Baker, Sanders, Maccotta, & Buckner, 2001; Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Buckner, Wheeler, & Sheridan, 2001; Casasanto et al., 2002; Clark & Wagner, 2003; Daselaar, Veltman, Rombouts, Raaijmakers, & Jonker, 2003; Davachi, Maril, & Wagner, 2001; Davachi, Mitchell & Wagner, 2003; Davachi & Wagner, 2002; Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Jackson & Schacter, 2003; Kensinger, Clarke, & Corkin, 2003; Kirchoff, Wagner, Maril, & Stern, 2000; Otten, Henson, & Rugg, 2001; Otten & Rugg, 2001; Ranganath et al., 2004; Reber et al., 2002; Rypma & D’Esposito, 2003; Sommer, Rose, Weiller & Büchel, 2005; Sperling et al., 2003; Stark &

Okado, 2003; Strange, Otten, Josephs, Rugg, & Dolan, 2002; Wagner et al., 1998) have identified subsequent memory effects in prefrontal cortex (PFC) and the medial temporal lobe (MTL) complex. A subset of these studies has examined the encoding that underlies source memory, memory for context, recollective memory or associative encoding and they reveal activations in MTL (Davachi et al., 2003; Davachi & Wagner, 2002; Sommer et al., 2005), PFC (Cansino, Maquet, Dolan, & Rugg, 2002; Henson et al., 1999) or both (Brewer et al., 1998; Kensinger et al., 2003) that are linked to subsequent successful associative, source or contextual memory performance.

The authors of these papers have proposed different processing roles for these regions (and subregions within them) that contribute separately to the formation of contextually bound, episodic memories. For example, Davachi and colleagues (Davachi, 2003) have isolated subsequent memory effects in hippocampus, and perirhinal, and parahippocampal (PHC) cortices. Importantly, the activated regions were dissociated by task (item recognition and source memory). Greater activation of hippocampus and left PHC at study was associated with accurate item recognition accompanied by correct source memory than with accurate item memory alone, but not with successful versus unsuccessful item recognition. Greater perirhinal cortex activation, on the other hand, was associated with correct recognition (item alone and item + source) than for missed items, but not with accurate source memory versus memory for item without source. Finally, Davachi and colleagues found that two regions of anterior left inferior prefrontal cortex were activated more during encoding of items for which source was subsequently correctly identified than for encoding of items that were subsequently recognized without recollection of source. Similarly, Davachi and colleagues (2002) found subsequent

memory effects in bilateral hippocampus for items encoded in a relational encoding task, but not during rote rehearsal.

In another study of the MTL and relational processing, Bar and Aminoff (2003) used fMRI to explore the recognition of strongly contextually identified objects (e.g., hardhat) with the recognition of items that have only weak contextual associations (e.g., fly). They found that portions of the parahippocampal cortex (parahippocampal place area or “PPA”) and retrosplenial cortex, areas previously identified in spatial processing and episodic encoding were activated more by recognition of strongly context-bound objects than objects that have only weak contextual associations. Moreover, they distinguished between anterior and posterior portions of the parahippocampal cortex that were associated more with non-spatial context recognition and with place-specific context recognition, respectively. They concluded that this PHC/RSC network might play a role in the formation of episodic memories by inputting to the hippocampus familiar associations established through experience (e.g., “which objects belong in a kitchen”). They speculated that this information is subsequently used by the hippocampus to represent specific instances (e.g., “which objects belong in *my* kitchen”) of this knowledge (citing Buckner, 2000). Taken together, these studies provide substantial evidence that MTL structures play an important role in the relational processing of verbal and visual pictorial stimuli for later subsequent retrieval of those relations. Bar and Aminoff have proposed that well-established general associative knowledge might be represented in a PHC/RSC network that is subsequently input to the hippocampus for participation in episodic encoding processes. The studies by Davachi and colleagues suggest that encoding of certain contextually related-information (i.e., processes engaged

during a verbal stimulus' original presentation) relies on different neural substrates (e.g., PHC/RSC) than the encoding of other relational information (e.g., semantic relations among verbal stimuli (hippocampus). These studies do little, however, to clarify whether the associative processes engaged by these different neural systems are mutually exclusive, the same or partially overlapping.

Henson and his colleagues (1999) and Brewer and his colleagues (1998) used Tulving's Remember/Know procedure to assess the phenomenological state associated with retrieval of old information. By sorting hemodynamic records at encoding that were associated with subsequent Remember or Know responses, the investigators attempted to measure indirectly the neural correlates of encoding associated with recollective or non-recollective states of recall (Henson et al., 1999). Although they found prefrontal subsequent memory effects associated with associative encoding, use of the Remember/Know technique may have confounded the subsequent memory effects associated with Remember and Know responses with the strength of item memory (Cansino et al., 2002). For example, in the study by Henson and colleagues, the procedure may have produced fewer Know than Remember hits and greater Know than Remember false alarms. If this is the case, Know responses may have represented guesses more than veridical memory responses.

In an effort to measure the phenomenological state at retrieval more directly, Rugg and his colleagues (Cansino et al., 2002) used a paradigm similar to that employed in ERP and fMRI studies of source memory. Cansino et al. had participants make animateness judgments to visually presented colored images. Each image was presented randomly in one of the four quadrants delineated on the computer screen. Following

encoding of the objects, a recognition phase was presented and participants pressed a button to indicate New or, if Old, a button corresponding to the location where the image had been presented. Cansino and colleagues found subsequent memory effects associated with associative encoding in right lateral occipital and left prefrontal cortex, among other areas. Consistent with earlier findings of Rugg and colleagues (Otten et al., 2001; Otten & Rugg, 2001) they argued that subsequent memory effects represent a subset of the neural activation required for encoding in any given task. They also claimed that the subsequent memory effects reflect the relatively greater semantic and perceptual processing received by certain items. Cansino and colleagues speculated on the relationship between perceptual and semantic processing contributions to the subsequent memory effects. They suggested that the perceptual and semantic processing may have contributed independently to the subsequent memory effects or, alternatively, greater perceptual processing may have been mediated by the occipital cortex and fed into the prefrontal cortex, allowing for more elaborated and, thus, better remembered, memory traces (Cansino et al., 2002). Interestingly, Cansino and colleagues failed to obtain subsequent memory effects in MTL, consistent with previous null findings by Rugg and colleagues (Otten et al., 2001; but see Otten & Rugg, 2001). They speculated that both Remember and Know responses may have reflected relatively high levels of hippocampal encoding related activity, or that the null finding simply reflected a lack of statistical power sufficient to detect such activity.

Finally, Kensinger and colleagues (2003) also measured indirectly participants' recollective state associated with memory for visually encoded words that were given semantic judgments ("abstract" or "concrete"). In an accompanying behavioral study,

participants made semantic judgments to visually presented words while performing either an easy or a difficult auditory discrimination task. Subsequently, participants were given a memory test and were required to make Remember or Know responses to words judged “old.” Kensinger and colleagues found a significant effect of distraction task (Easy vs. Hard) as well as an interaction between distraction task and memory strength (Remember vs. Know). They concluded that the task manipulation altered the type of memory trace formed and used the distraction task, (followed by a yes-no recognition task, also performed under distraction), as the independent variable in the imaging experiment. Kensinger and colleagues found subsequent memory effects in bilateral PFC and left MTL. However, in left PFC, these effects were for items encoded only under easy distraction, whereas right PFC subsequent memory effects were obtained for encoding under both easy and difficult distraction conditions. Likewise, PHC activation predicted subsequent memory performance under both distraction conditions whereas left anterior hippocampal activation predicted subsequent retrieval only for items encoded under easy distraction. The investigators concluded that the formation of detailed, contextually rich memory traces depends on activation of the left PFC and left anterior hippocampus. They also concluded that the formation of contextually rich, detailed traces depends on the activation of a subset of the neural processes activated by successful encoding generally.

Habib and colleagues (2003) recently reevaluated the Hemispheric Encoding and Retrieval Asymmetry (HERA) model proposed by Tulving and colleagues (Nyberg, Cabeza, & Tulving, 1996; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). They concluded that existing PET and fMRI data still support the conclusion that the left PFC

shows greater activation in encoding tasks (relative to retrieval tasks) than the right PFC. Conversely, the right PFC shows greater activation during retrieval tasks (relative to encoding tasks) than the left PFC. They asserted that such a process-specific lateralization could co-exist with the material-specific (e.g., verbal vs. non-verbal materials) lateralization, observed by a number of investigators. Habib and colleagues reiterated the notion that the preferential left PFC activation during episodic encoding is likely to be associated with semantic processing of incoming and on-line information. Recent work involving transcranial magnetic stimulation (rTMS) supports HERA showing disruptive effects to encoding by application of magnetic pulse trains to left PFC and degradation of retrieval by application of magnetic pulses to right PFC (Rossi et al., 2001).

Thus, there is conflicting evidence as to whether the right prefrontal cortex is involved in associative encoding. There are few fMRI studies of long-term memory studies that show right PFC subsequent memory effects, and the HERA model accords the left PFC a predominant role in LTM encoding. In contrast, a few ERP studies (Kounios et al., 2001; Schott et al., 2002; Weyerts et al., 1997) have identified subsequent memory effects at *right* prefrontal electrodes for associative encoding. Furthermore, the right PFC finding in these studies is supported by fMRI findings of Prabhakaran and his colleagues (2000) and Johnson and her colleagues (Mitchell et al., 2000a) in working memory studies of object and location binding. The role of the processes underlying these effects is still controversial.

The Present Investigation

One challenge, therefore, is to (1) examine the creation of memorable episodes by identifying those cognitive and neural processes that link events and their contexts; and

(2) determine whether or not those processes are consistent with the current theoretical accounts of the relationship between working memory and episodic memory. The experiments presented in this dissertation are an attempt to tackle a piece of that challenge. The first purpose of this dissertation is to test whether associating concrete, highly imageable items and complex contextual scenes into events (e.g., elephant at an intersection) in working memory is a key component of successful long-term episodic memory performance. The second purpose of this dissertation is to test whether successful long-term memory “binding” produces a temporally and topographically unique electrocortical “signature” during working memory that distinguishes it from unsuccessfully bound items and contexts as well as from unbound, but remembered, items and contexts.

CHAPTER 2

EXPERIMENT ONE

As described above, there is substantial evidence that the neural underpinnings of the relational binding (both episodic and associative) which subserve long-term memory can be observed by two basic strategies: a comparison of encoding tasks that do, and do not, require some sort of relational or contextual encoding between elements; and a post-hoc sorting of encoding events that do, and do not, result in subsequent memory for contextual versus item information. But there is little consensus about the conditions that produce such a binding “fingerprint.” Moreover, the details (timing and topography) of the fingerprint are even less obvious, in large part due to the inconsistency with which subsequent memory effects are detected.

One likely source of this inconsistency is the wide variety of encoding tasks, on the one hand, and ways of assessing memory, on the other, that have been used by different researchers. In some cases, for example, the relational task is qualitatively different from the nonrelational task on dimensions other than relational processing as such. More challenging memory tasks (e.g., recall) and test responses that reflect more elaborative memories (e.g., “Remember” vs. “Know” responses) more often produce subsequent memory effects than simple yes - no recognition, but at the same time, are themselves complex enough to introduce constructive and inferential processes at retrieval that may interact with any encoding processes being studied.

In each of the present experiments, a simple yes-no recognition task was used to minimize the role of retrieval factors in any subsequent-memory effects. As importantly,

a task was adopted in which the encoding processes were as similar as possible, while some groups attempted to integrate the two stimuli, and others did not.

The materials. Concrete, imageable words, as well as pictures, have been shown to elicit Dms, whereas abstract words and symbols are less likely to produce subsequent memory effects. The requirements of the stimulus materials were three-fold. First, they had to consist of familiar, integrable, item and spatial location pairs. Second, they had to produce sufficient levels of recognition failure during a paired recognition test. Third, in contrast to the materials of Craik (1989), each item (and pair) had to be unique, to avoid potential cross-pair interactions during either encoding or retrieval that could complicate the subsequent-memory analysis. As discussed below, the stimulus materials selected fulfill each of the foregoing criteria.

The task. An experimental task in which participants were required to associate (bind) unique spatial locations and objects was contrasted with a condition in which participants would be required to process the same materials in the same way without integrating the two. Following Bower (1970), a task was designed to promote integrative encoding in a paired recognition task.

Expected Results.

Following Bower (1970), we expected that the overall pattern of results for paired recognition performance between the two groups (Bound and Separate) would reflect better recognition of previously presented pairs by the group that formed integrated images (Bound) than by the group that maintained separate images (Separate). Overall, we expected the between-group manipulation to produce similar ERPs at encoding – due to the identity of the stimulus materials and the similarity of the experimental conditions between the two groups. We anticipated that distinctive between-group ERPs would most

likely be reflected to the second word – at which point the integrative processing in the Bound, but not the Separate, condition could begin. Alternatively, however, task-related ERP contrasts could be associated with attentional or other “set” differences. These differences could show up as broader differences in the ERP patterns encompassing the first word, and even the pre-stimulus interval. However, we predicted that, in addition to differences in the second word interval, the task manipulation would be most likely to reflect differences late in the first word interval, as participants prepared for the second word. In any event, we expected ERP task differences to be minimized by our decision to manipulate the task as a between-subjects factor, thus producing significantly more variability for it than for the within-subjects factor (memory performance).

While we expected the overall pattern of results between the two groups to be similar, primarily yielding differences following the second word – where integrative processing would be reflected in Bound but not Separate ERPs - we anticipated that the subsequent memory effect differences (Dms) would reflect the relative role of the first and second words in associative encoding.

In this regard, our method provides a unique advantage over previous paradigms that have used a limited number of associative possibilities (male/female voice; limited spatial locations, etc.). Thus, the “binding” or relational processing could only take place upon presentation of the second word. Consequently, we expected a unique signature in the Dm to the second word for cases in which paired recognition failure was a result of unsuccessful binding of the object and location. Given that several of the few experiments in which Dms were produced for associative or elaborative processing yielded frontal Dm effects (Duarte et al., 2004; Fabiani et al., 1990; Fernandez et al.,

1998; Karis et al., 1984; Kounios et al., 2001; Mangels et al., 2001; Schott et al., 2002; Weyerts et al., 1997) we anticipated that associative subsequent memory effects would be produced to the second, but not the first, word, at frontal electrode sites, with right frontal locations possibly showing greater effects than left. Moreover, we expected these differences to begin later in the interval (~1000 ms after word 2 onset) and be sustained throughout the interval.

We also predicted that a set of frontal transient Dms, similar to those observed by Mangels and colleagues (2001) and Duarte and colleagues (2004), beginning as early as 400 ms following word onset, might be produced to both the first and second words. Based on previous findings, these earlier Dms would likely be either left-lateralized or bilateral.

Method

Participants

Seventy-four undergraduates (47 females) at the University of Florida participated in this experiment. Additionally, 37 undergraduates participated as pilot participants during development of the tasks and materials. Twenty-two of these pilot participants were used to ensure that Bound and Separate encoding produced different levels of subsequent memory performance and the stimulus delivery and data recording program was operating as anticipated. Fifteen additional pilot participants were used to test the effectiveness of an alternative instruction directing participants to respond "old" only if they were sure that they had seen the pair as presented before. Participants were randomly assigned to the two experimental groups. Participants received credit toward an introductory psychology course requirement. Of the 74 participants who began the experiment, three left without completing the test phase so neither behavioral nor EEG

data were useable for those participants. 11 other participants had too few (< 10) incorrect responses to the memory test portion to permit construction of reliable (based on visual inspection) waveforms. Finally, as discussed in the Results section, of the remaining 60 participants, various technical and signal-to-noise problems prevented analysis of another 21 EEG datasets.

Materials and Apparatus

Stimulus display and response recording

The entire experiment was administered in a small, dimly lit room (approximately 5.5' x 6.5') on a personal computer using a conventional CRT monitor with a screen size of approximately 13" measured diagonally. Participants were seated about 24" from the monitor. A program written in the Delphi programming language (Borland Software Corp.) controlled stimulus presentation and recording of behavioral responses.

Participants viewed stimulus items in the middle of screen and responded to stimulus events by using a standard two-button mouse. During the recognition phase, participants made affirmative recognition responses by pressing the left mouse button and negative responses using the right mouse button.

EEG recording

Electroencephalographic activity (EEG) was recorded using a standard elastic cap (Electro-Cap International, Inc.) with 13 embedded tin electrodes placed in standard 10-20 system (Jasper, 1958) locations (Fp1, Fp2, F3, F4, FT7, FT8, Cz, TP7, TP8, P3, P4, O1, O2). The cap was linked to a set of bioamplifiers (SA Instrumentation Co.). Data were filtered (high pass - 0.01 Hz; low pass - 50 Hz), amplified 50K, digitally converted using National Instruments analog to digital converter and stored for subsequent off-line analysis. In addition to the scalp-recorded EEG, horizontal electro-oculogram (hEOG)

was recorded with a pair of tin electrodes placed on the outside canthus of each eye. A second pair of tin electrodes placed above and below the left eye recorded vertical EOG (vEOG). The gain for both EOG channels was 20K. A third pair of tin electrodes was placed on the skin above the mastoid bone behind each ear. During recording, Cz was used as a common reference for all other scalp and mastoid sites. During subsequent data analysis, the EEG was rereferenced to the average of the left and right mastoid sites. The sampling rate throughout the experiment was 100 Hz.

Stimulus materials

The stimulus materials consisted of 360 words drawn from various sources (Battig & Montague, 1969, Rubin & Friendly, 1986) and experimenter-generated items. These words were evenly divided between location and object (people, animals, inanimate objects) words. We reduced original lists of locations ($n = 283$) and objects ($n = 656$) by eliminating rare (e.g., boomslang, oceanographer) or difficult to image (e.g., albatross, charlatan) items as well as obvious synonyms (e.g., physician, doctor; ocean, sea) or category-exemplars (sheep – lamb; spider - tarantula). The resulting lists were submitted to the MRC Linguistic database (http://www.psy.uwa.edu.au/MRCD DataBase/uwa_mrc.htm) to obtain normative data on written word frequency, imageability, meaningfulness, and concreteness. Outliers (± 2 s.d.'s from μ) were excluded. The final list of 160 pairs consisted of various objects, including people/occupations ($n = 41$), animals ($n = 47$), tools ($n = 14$), vehicles ($n = 14$), toys ($n = 10$), weapons ($n = 13$), musical instruments ($n = 8$) and furniture ($n = 13$). These people, animals and inanimate objects were paired randomly with locations and were manually examined to eliminate pairings with obvious pre-experimental associations

(bartender – bar; clown – circus). Once was the list of 160 pairs was generated, one-half of the pairs were re-sorted to produce a test list consisting of 50% intact and 50% rearranged pairs. In the test list, the intact and rearranged pairs consisted of approximately the same number of object types described above.

Design

The design for the study phase was a single factor (Encoding Task: Bound versus Separate encoding of the words in a pair) between-subjects design. During the test phase, all participants were given the paired recognition test.

Procedure

After giving informed consent to the procedure, participants were fitted with the electro-cap and other electrodes. Generally, impedances, measured against Cz, were kept under 8K Ohms. Once participants were prepared for EEG recording, the experimenter gave an overview of the experimental procedure (i.e., “You’ll be viewing words presented on the screen and generating mental images of each of the words. You’ll rate the ease with which you generated the image. Following the image generation task, you’ll be given a memory test for the words.”). Following this instruction, participants read, on the screen, a more detailed set of instructions regarding the study phase.

In brief, all participants were instructed that they would view pairs of words, each consisting of, first, an object (person, animal or object) and, second, a location. Participants were instructed to generate and maintain a “rich, vivid” visual image of the word’s representation upon its presentation. Participants were instructed to rate, following the location word, the ease with which they generated the image(s). For this purpose, participants were shown, on the screen, four clickable radio buttons captioned with a rating scale (Really easy, Somewhat easy, Somewhat difficult, Really difficult).

Participants were instructed to make this judgment relatively automatically, giving their “first impression.” Instructions between the two (Bound/Separate) groups differed only regarding the generation of the image(s). Participants assigned to the Bound group were instructed to generate a mental image in which the first word (object/person/animal) and the second word (location) were integrated into a single image or scene. They were instructed to make this “scene” as visually rich and vivid as they could. Participants assigned to the Separate group were instructed to maintain the image of the object and the location separately. Specifically, it was suggested that participants “place the image of the [first word] on the far left side of your “imaginary visual field and the image of the [second word] on the far right side of the imaginary visual field.” Virtually all participants expressed comprehension of this instruction. The experimenter eliminated any confusion with further explanation.

As displayed in figure 2-1, the study phase, and each trial, commenced with a fixation cross, displayed for 300 ms, followed by a 700 ms post-fixation interval during which the screen was blank. Following the post-fixation interval, participants viewed words, presented singly in 28-point Arial font, each displayed for 500 ms with a 2500 ms interstimulus interval (ISI). EEG recording began 100 ms following offset of the fixation cross, and hence 600 ms prior to onset of the first word of each pair, and continued through 2600 ms after onset of the second word. Following the second word ISI, the ratings buttons were displayed until the participant selected one. The intertrial interval (ITI) between this mouse press and initiation of the next trial was fixed at 1000 ms. Following the presentation of each forty consecutive trials, the program paused for a

participant-paced rest. Most participants, however, continued the experiment without a significant rest period. At the end of 160 trials, the program stopped.

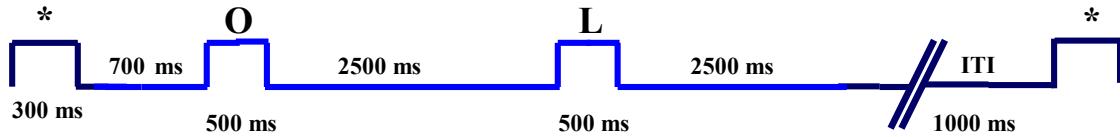


Figure 2-1. Schematic representation of a single trial during the study phase in Experiment 1. * is fixation cross, “O” and “L” are presentation of object and location words, respectively. “//” is the self-paced, response interval during which participants indicated the ease of image generation. “ITI” indicates intertrial interval. Light colored line is EEG recording interval.

The experimenter then engaged the participant briefly in unrelated conversation to prevent overt rehearsal of the last few presented items and to give the participant a brief break (~ 5 minutes) from the task. Thus, the mean latency from a pair’s appearance in the study phase to its appearance in the test phase was approximately 40 minutes.

The timing and appearance of stimulus items in the test phase was the same as in the study; viz, a fixation cross, an object word, and then a location word were presented. However, the interstimulus interval between object and location words was reduced to 1500 ms and only a single break (rather than the three in study phase) was provided. Participants in both conditions (Bound/Separate) were instructed to indicate, using the left mouse button for affirmative responses and the right mouse button for negative responses, whether the OBJECT-LOCATION pair had been shown earlier (yes – left mouse button) or whether the pair consisted of an object and location that had been paired earlier with other items (no – right mouse button). Participants were instructed to make these responses as quickly as possible due to the measurement of response times. Following the old-new mouse presses, the monitor displayed a three-choice alternative

(“The second word presented,” “Another word not presented,” “No other word”) to which participants were instructed to respond. The participants were told to respond according to their reaction to the first (object) word of the trial. That is, if presentation of the first word immediately elicited a word, participants were instructed to click on one of the first two choices (depending on the second word that was presented). On the other hand, if the presentation of the first word failed to elicit another word, participants were instructed to select “No other word.”

Results

Behavioral Data

As expected, participants in the Bound condition were better at discriminating intact pairs from rearranged pairs (hits: $M = 59.1$, $SE = 1.66$; false alarms: $M = 9.0$, $SE = 1.33$) than participants in the Separate condition (hits : = 46.5, $SE = 1.87$; false alarms: $M = 26.7$, $SE = 2.54$) during the test phase, $t(37) = 11.50$, $p < .001$. Performance differences between the two groups were not attributable to speed-accuracy tradeoff; the groups did not differ in their correct response times to intact pairs (Bound: $M = 1341$ ms, $SE = 69$; Separate: $M = 1337$ ms, $SE = 64$, $p > .10$). These findings, coupled with participants’ post-hoc comments to the experimenter, suggest that they were, at least overall, generating and maintaining integrated or separate images in the two conditions as instructed.

EEG Data Preprocessing

Prior to averaging, the raw EEG data were inspected manually for the presence of blinks and other artifacts on a trial-by-trial basis. In the next phase, EEG for each trial was digitally low-pass filtered at 30 Hz for smoothing, and the mean amplitude set to zero for that trial to correct for baseline shifts. During this phase, trials marked as

containing artifacts were subjected to a componential analysis and reconstruction process to attempt to remove blink and other artifacts from the waveforms, using the Independent Component Analysis (ICA) procedures and routines from the EEGLAB toolbox (Delorme & Makeig, 2004), and a locally written Matlab script. Typically, one or two components were clearly identifiable with blinks/artifacts, and successfully removed. A maximum of four components (out of 16, limited by the number of recording sites) were allowed to be removed before rejecting the trial as unusable.

ERP waveforms

ERPs elicited by word pairs in the study phase were, as noted, computed on the basis of participants' responses on the subsequent paired recognition test. Data from the study phase were sorted according to the following test phase responses: "old" responses to intact pairs were classified as IC (Intact Correct); "new" responses to intact pairs were classified as IE (Intact Error); "old" responses to rearranged pairs were classified as RE (Rearranged Error); and "new" responses to rearranged pairs were classified as RC (Rearranged Correct). As noted above, a large number of participants' data were excluded from analysis to be presented here. Thirty-nine participants (19 Bound/20 Separate) provided data for the analysis described below. Each participant's averaged data were then averaged with other participants' averaged data to calculate grand averaged data for each class. Baseline adjustment (setting the mean amplitude during a prestimulus interval for each condition equal to zero) was not performed, since it was possible that important ERP differences between various classes, including between pairs that were subsequently recognized and those that were subsequently forgotten, might be reflected in the prestimulus interval.

ERPs to the Bound condition from the 13 scalp electrode sites are presented in Figure 2-2 below. The black line indicates ERPs for subsequently recognized intact pairs (IC), and the grey line indicates ERPs for intact pairs erroneously identified as re-paired (IE). Over the course of the 6200 ms interval, early event-related potentials (N100, P200, N400) to each word are clearly visible across most channels, followed by a broader later positivity around 600 ms, and a slow wave whose direction and magnitude differed widely across channel, and sometimes continues through the end of the epoch for each word.

Differences as a function of subsequent memory performance can be seen later in the interval during the slow wave epoch, which appear greatest bilaterally at the frontal electrodes. For example, at the frontopolar (Fp) electrode sites, a sizeable difference between IC and IE traces is noted beginning at about 1600 ms from the beginning of the interval (1000 ms post-first word onset). Interestingly, in this case, correctly recognized pairs show a greater negativity during the interval than do subsequently forgotten pairs. The difference lasts until about 4000 ms when a significant reversal is noted, with IE becoming more negative than IC. A small difference between IC and IE is also visible during the earliest part of the interval (prestimulus through word one presentation), particularly at the frontal electrodes.

The waveforms to the Separate condition (Figure 2-3) show marked contrasts to those from the Bound condition. There is little visible difference between the IC and IE waveforms. The large, slow wave differences between IC and IE that are present beginning in the 1000 ms range in the Bound condition are absent in the Separate condition. As with the Bound condition, however, activity at the frontopolar sites is

distinguished, for both IC and IE responses, from the activity at all other locations by a positive, slow change beginning about 1600 ms from the beginning of the interval. Other locations are characterized either by a negative change during the interval, or by no change. Additionally, the Separate waveforms are distinguished from the Bound waveforms, especially at frontopolar sites, by the presence of two distinct positive peaks following the presentation of each word. The first of these peaks would appear to be a P200 to the onset of the words. The second positive peak is close to 200 ms after the offset of the word (after 500 ms) and may well be an offset response to the offset of the stimulus (see, e.g., Janata, 2001).

Finally, a comparison between the IC responses to the Bound and Separate conditions is presented in Figure 2-4. Waveform differences between the IC responses that are evoked by the different task demands are apparent, if small. The second half of the last interval (~5500 ms) appears to show differences between the two correct responses in the right hemisphere. In addition, FT7 appears to reflect a difference between the IC responses that mimics, temporally, the differences observed at the frontopolar sites between IC and IE responses in the Bound condition. In addition, early, prestimulus differences between Bound and Separate IC responses are similar to those accompanying IC-IE responses in the Bound condition.

Statistical analysis of waveforms

Visual inspection of the grand averaged waveforms led us to identify windows of interest for subsequent statistical analysis. Subsequent memory effects were quantified by measuring mean amplitudes during each of ten successive latency intervals relative to onset of each word ([w1] -600 - 0, 0 - 300, 300 - 600, 600 - 1200, 1200 - 2600; [w2] -400

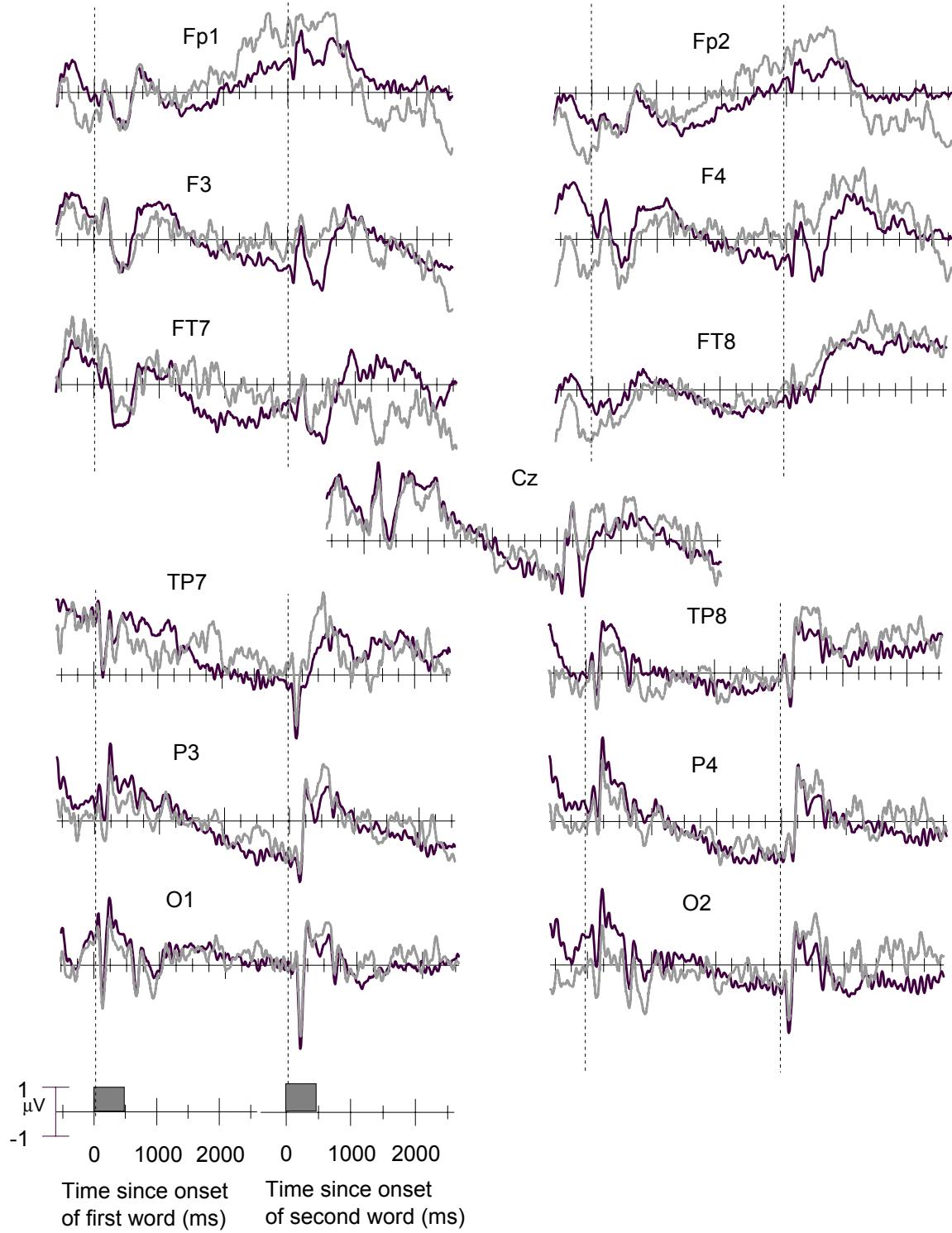


Figure 2-2. ERPs to two words during study phase later shown as intact pairs during test in Experiment 1, Bound Encoding group. Bars indicate onset and offset times of the words. Black waveform is for pairs later correctly recognized as intact; grey waveform is for pairs later misrecognized as repaired.

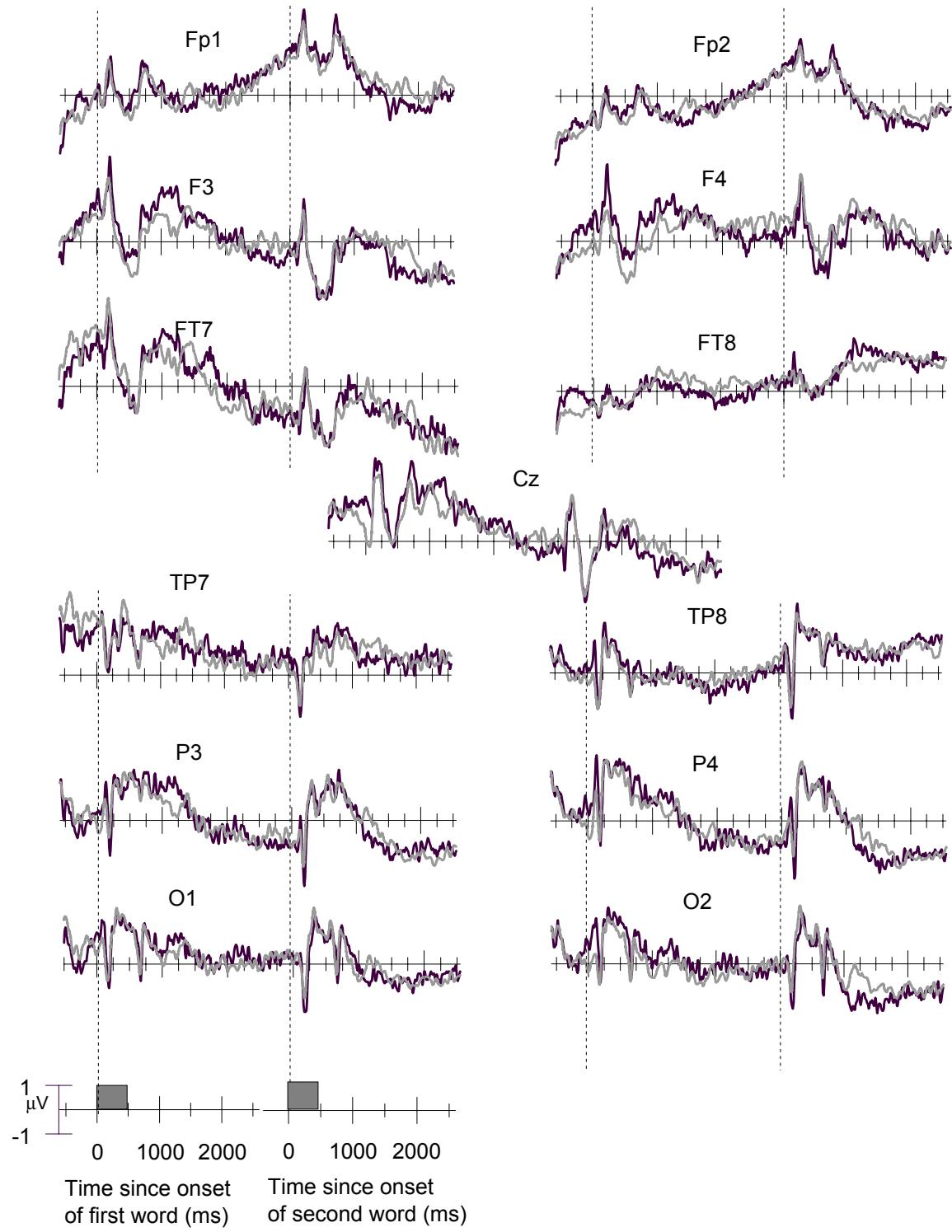


Figure 2-3. ERPs to two words during study phase later shown as intact pairs during test in Experiment 1, Separate Encoding group. Bars indicate onset and offset times of the words. Black waveform is for pairs later correctly recognized as intact; grey waveform is for pairs later misrecognized as repaired.

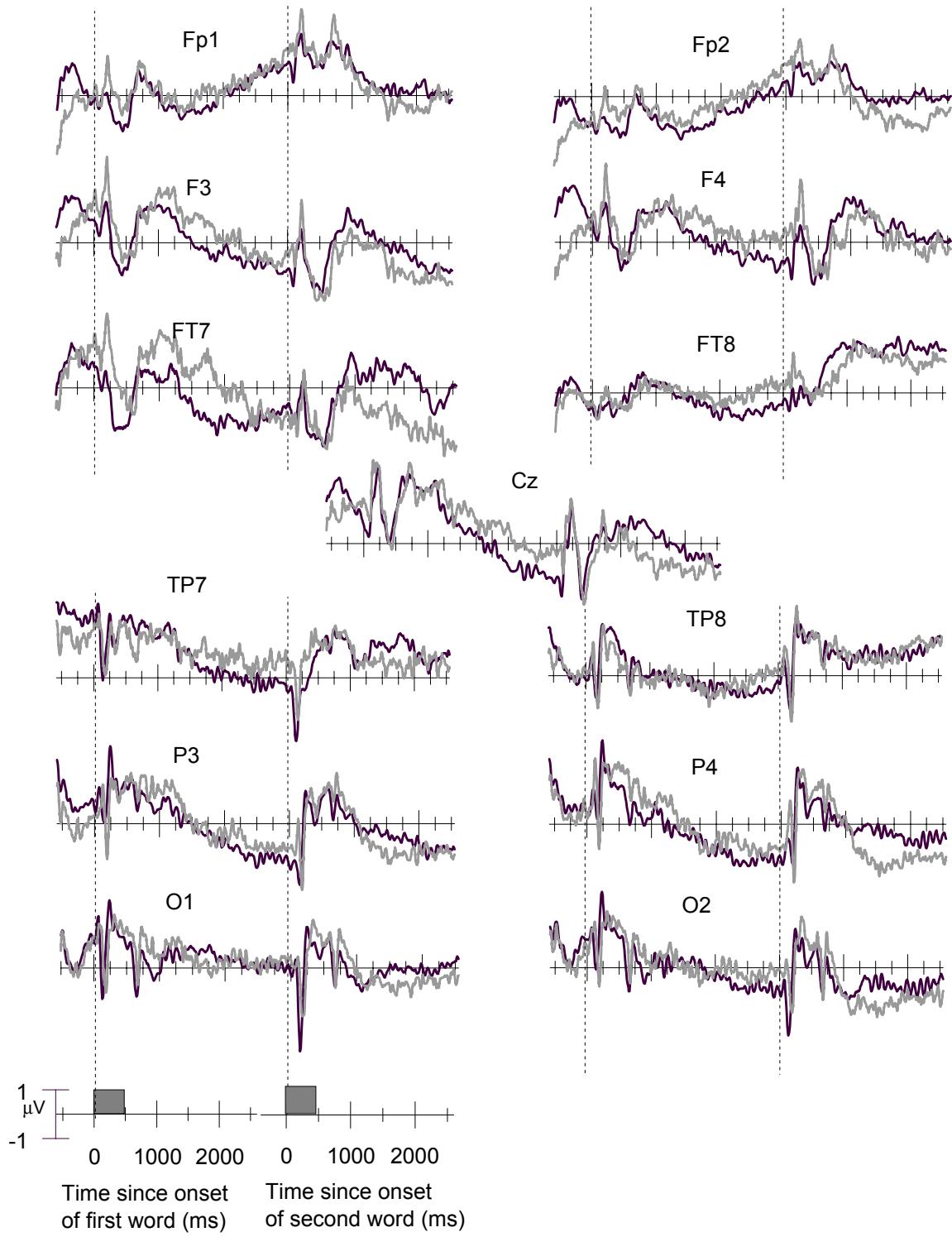


Figure 2-4. ERPs to two words during study phase later shown and correctly recognized as intact pairs during test in Experiment 1. Bars indicate onset and offset times of the words. Black waveform is for the Bound Encoding group; Grey waveform is for the Separate Encoding group.

- 0, 0 - 300, 300 - 600, 600 - 1200, 1200 - 2600 ms). Initial analyses were conducted by running, for each condition (Bound and Separate), an analysis of variance (ANOVA) on the mean interval amplitudes of ten “windows” that comprised the total 6200 ms trial interval to test whether they differed across the selected factors. In addition to the subsequent memory factor, two regional EEG factors were created from the 12 lateralized sites, excluding Cz. The ANOVAs thus utilized a 3-factor (Performance: Hit/Miss; Hemisphere: Left/Right; Anterior-Posterior (“AntPos”): 6 levels of electrode site), $2 \times 2 \times 6$, within-subjects design. In addition, a third set of ANOVAs was run to compare the mean amplitudes produced by correct responses to intact pairs between the Bound and Separate conditions in each window. Thus, this ANOVA was a 3 factor (Task: Bound/Separate; Hemisphere: Left/Right; Anterior-Posterior: 6 levels of electrode site), $2 \times 2 \times 6$, mixed design. In all analyses, the Greenhouse-Geisser correction (ϵ) was applied for violations of the assumptions of sphericity for comparisons involving two or more degrees of freedom.

Bound condition

As presented in Table 2-1, in the Bound condition, there were two intervals that yielded significant interactions involving subsequent memory. In the long interval (1200 – 2600 ms) between presentation of the first and second word there was a significant interaction between Performance and the AntPos factor, $F(5, 90) = 3.68$, $p = 0.013$, $\epsilon = .696$, reflecting the larger subsequent memory effects across the frontal electrodes than at the more posterior sites. A second ANOVA which analyzed only the differences between the right and left Fp electrodes (excluding the other electrode sites) revealed no differences between the hemispheres ($p > .10$). Differences similar to those found to the first word were observed, in the form of a significant Perf x AntPos interaction, $F(5,90) = 5.671$, $p =$

0.005, $\epsilon = .452$, in the comparable interval (1200 - 2600 ms) to the second word. This interaction reflects, again, the larger Dm in the frontal sites. However, unlike in the Dm to the first word, the amplitudes of IC items are more positive than of IE items. Finally, there was a main effect of Performance

Table 2-1. Time Intervals in Experiment 1 during which Amplitude Differences were Significant

Interval	Factor		
	Perf	Perf x AntPos	Perf x Hem
[w1]-600 - 0			S
0 - 300			
300 - 600		H	
600 - 1200			
1200 - 2600		B	
[w2]-400 - 0	S		
0 - 300			
300 - 600	B		
600 - 1200			
1200 - 2600		B	

Note. “B” = significant Dm effects in Bound task, “S” significant Dm effects in Separate task, “H” = significant differences in Bound – Separate correct recognition (Hit) comparison. For all comparisons, $\alpha = .05$.

in one of the early intervals (300 - 600 ms) to the second word in which the IE items were more positive than the IC items. Thus, quantification of the mean amplitudes through the various time windows that make up a single trial revealed subsequent memory effects that were larger toward the frontal part of the scalp than toward more posterior regions. Moreover, these effects appeared at approximately the same latency following the onset of each word. Finally, a more generalized Dm was observed early after the onset of the second word.

Separate condition

The Separate condition yielded significant Dm effects at two intervals, neither of which overlapped with the effects observed in the Bound condition (Table 2-1). A significant Perf x Hemisphere interaction was observed in the prestimulus interval (0 - 600 ms), $F(1, 1) = 6.162$, $p = 0.023$, $\epsilon = 1.0$, reflecting the greater right-sided Dm in the prestimulus interval. A second Dm effect was observed in the -400 – 0 ms interval, just prior to onset of the second word. This effect did not interact with either of the other factors, $F(1, 19) = 4.862$, $p = 0.040$, $\epsilon = 1.0$.

Bound vs. separate conditions

The final analysis run in the first experiment was to compare the IC responses produced in the Bound and Separate conditions. A significant interaction between the Task factor and AntPos occurred in the first word interval at 300 – 600 ms [$F(5, 90) = 4.332$, $p = 0.021$]. This interval captures the temporal window during which the N400, and P300 components typically are observed. There is little consistency reflected in this particular interaction; Differences are noted between frontal and posterior sites and the effects of task are opposite to one another between the two.

Discussion

Following Bower (1970), participants showed impaired recognition performance after encoding items in the Separate, compared to the Bound, task instructions. This shows that even with the co-presentation of a given pair of words, and their high imageability, participants in the Separate task were, to a great degree, capable of keeping the two items separate and distinct, as instructed. Moreover, when queried, all participants in the Bound condition reported being able to “bind” the object and location into a single image. Likewise, all participants in the Separate condition reported being

able to generate and maintain object and location images separately. Occasional participants in the Separate condition reported that “on a couple of trials” they “couldn’t help putting (binding) the images together.” These reports were sporadic and no participants reported this “problem” to have occurred on more than 2 or 3 of the 160 study pairs. Thus, the instructions to generate and integrate and object and location in the Bound Condition (and generate and maintain unique images in the Separate condition) can be assumed to have acted as intended.

As expected, we obtained reliable subsequent associative memory effects using a task that places demands on associative encoding. Participants were instructed, in both the Bound and Separate conditions, to generate mental images that were as clear and visually rich as possible. We anticipated that the instructions in both conditions would promote extensive cognitive effort by participants that would yield observable differences between later forgotten and later remembered pairs. We hypothesized that successful pair recognition would depend on (a) adequate processing of each element (object and location) of the pair, and (b) the creation and maintenance of a link between the two. Thus, the strongest prediction that we made was that the Bound condition would reveal transient frontal Dm effects that would appear in response to each word, as well as a later-appearing Dm in response to the integrative demands of the task. On the other hand, we predicted that the Dm effects for the Separate condition would follow from the lack of integrative instructions in the task. We expected any subsequent memory effects to reflect the establishment of strong memory traces for the objects and locations individually and there should be no late, frontal, second-word-only effects associated in the Bound condition with integrative activity.

The Bound condition ERPs revealed a striking pair of subsequent memory effects that occurred with the same latency following onset of the first word and the second word (1200 – 2600 ms) and the same largely symmetric frontal topography. Notably, however, the relative polarity of the difference was the opposite between the first and second word late Dm effects. That is, the Dm to the first word was negative (Bound < Separate) and the Dm to the second word was positive (Bound > Separate). Although the negative Dm has been identified in only one other study (Dm for name recognition - Guo, 2005), we can speculate, in the present case, why it may have occurred. Our particular paradigm has some similarities to a CNV-producing S1-S2 (Go No-Go) paradigm. Therefore, as noted, we expected to find a “slow wave” component, analogous but not identical to the CNV, between the first and second word. We assumed that this slow wave might show significant amplitude shift. In the current study, we noted that this slow wave activity appears over several electrode sites. We pointed out, however, that the shift was in a positive direction only at the Fp sites. If the positive change at the Fp sites reflects a preparatory, maintenance-like state (similar to the E-wave of the CNV), then the greater negativity of the hits (relative to the misses) at the Fp sites might reflect ongoing processing of the first word and/or preparation for the second word that underlies successful binding. Conversely, the greater positivity of the hits in the late interval following the second word is more typical of a Dm effect and, perhaps more expected, in light of the fact that the final word of the pair has been presented and the participant need anticipate no further events in the trial. Thus, the later (1200 – 2600 ms) second-word Dm could reflect both the processing of the second (location) word and the establishment of a successfully integrated trace.

We also noted the presence of a third, widespread Dm in the Bound condition, occurring just after the presentation of the second word (at 300 ms) but not after the first word, which suggests that the cognitive processing associated with the late (1200 ms) second-word Dm may not have reflected identical processing to that during the earlier (1200 ms), first-word Dm. This difference is reflected in a greater positivity for subsequently missed pairs than for subsequently recognized pairs. It could be that the early, second word Dm reflects the initiation of cognitive mechanisms to respond to the integrative task demands, or the assessment of the presented location as appropriate for integration. Although it is not entirely clear, it appears that the differences at this interval are from a reduction in the N400, an enhancement of the P300, or some combination of the two in the later-missed items.

Unexpectedly, however, the Separate condition also revealed a temporally similar (-400 ms) widespread second-word Dm effect. The timing is especially surprising. Two possibilities seem plausible. One possibility is that, despite instructions to keep the images of location and object separate, participants were, in fact, integrating the two. Thus, the Dm at the end of the first word interval could reflect preparatory activity for binding the just-presented object word to the to-be-presented location word. This conclusion, however, seems unwarranted for at least two reasons. First, participants in the Separate condition reported that they were successful in generating and maintaining separate images for the object-location pair. The significantly poorer recognition rates for the Separate condition further supports their contention. Second, there is no ERP evidence, in the form of a Dm effect, that participants are doing anything during the second word that distinguishes remembered from forgotten pairs. An alternative, more

plausible, explanation is that the late, first-word Dm in the Separate condition represents further processing of the object word or a preparatory attentional shift or disengagement from the first word in anticipation of the second word. This attentional shift effect would be expected to be present in the Separate condition, if an adequate trace was established to the first word, but not in the Bound condition where the object and location are required to be integrated. In any event, the pattern of Dm effects shows differences in timing and topography between the two experimental conditions, reflecting the likely engagement of a different set of neural and cognitive processes that yield success or failure in each condition.

Finally, the lack of differences between the IC responses in the Bound and Separate conditions, except along a brief, early 300 ms interval to the first word, is somewhat unexpected. Our strongest prediction was that the integrative activity, present in the Bound but not the Separate task, would have discernable effects on the scalp related ERPs. Given the temporal and topographical differences between the Dms in the Bound and Separate conditions, we expected that the correctly recognized, intact pairs would likewise show differences between the Bound and Separate conditions. The lack of differences between the groups may be attributable to greater variability between the groups than the within-group variability in the Dm comparisons.

Nevertheless, the pattern of subsequent memory differences associated with paired recognition of objects and locations provides important evidence that areas of the prefrontal cortex have an important role in establishing the relationship between the items. This electrophysiological response occurs following both the first and second words and is consistent with a variety of accounts (e.g., Craik, 1989; Hunt & Einstein,

1981) of memory encoding suggesting that relational processing has a separate cognitive basis from item processing. In the second experiment, we used the same materials and instructions but gave participants an item recognition test to examine the event-related potentials associated with subsequent memory success.

We anticipated that, if the pattern of ERP Dms we identified in the first experiment were associated with relational encoding, a different pattern of Dm effects would be present for the item recognition test.

CHAPTER 3 EXPERIMENT TWO

The first experiment demonstrated some physiological evidence of the cognitive underpinnings of episodic encoding. However, by its design, the experiment left unclear whether the subsequent memory effects that were identified were those capable of supporting single item recognition, associative recognition alone, or both item and associative recognition. The second experiment attempted to isolate the processes that support subsequent item recognition and contrast these from processes that support associative recognition. We used the same materials and task at study as in Experiment 1. However, the subsequent recognition test was for individual words presented as objects or as locations during the study phase. Memory for objects and locations were tested separately to enable the creation of ERP records that could be conditionalized on either object recognition or location recognition.

Expected Results

We anticipated that the Bound versus Separate manipulation would have little impact on overall performance on the memory test. That is, item recognition would be relatively unaffected by whether participants attempted to integrate objects and locations at study. Given that participants in both conditions utilized similar semantic encoding strategies and were both instructed to make their visual images “as rich and vivid as possible,” we presumed that there would be no difference in item recognition levels.

We expected that the ERPs in the Bound condition, conditionalized on subsequent item recognition, would be associated with the processing of individual items, not with

the integration of objects and locations. Consequently, we anticipated little difference between the Bound and Separate Dm effects. Moreover, our design, which tested object and location recognition separately, enabled us to isolate ERP correlates of subsequent performance associated with each item of the studied pair. Thus, we anticipated, for example, that an object recognition test would yield subsequent memory effects associated with the prior presentation of objects, but not locations. If, as we posited, the Dms in Experiment 1 were associated with relational encoding, the Dms isolated in the current experiment should differ from those in Experiment 1 by timing, topography, or both.

Given the inconsistent findings as to topography of Dm effects in item recognition, we make no specific predictions about the likely topography of Dm effects in the current experiment. However, the findings from Experiment 1 and the existing Dm literature provide some guidance as to the anticipated timing of Dm effects. Given that Dm effects putatively associated with relational encoding occurred in the long (1200 – 2600 ms post word 1/post word 2) intervals in Experiment 1 we anticipated that item-specific Dm would be associated with earlier intervals and show greater transience.

As in Experiment 1, we expected the difference between the task-specific ERPs (Bound correct responses vs. Separate correct responses) to be minimized by the increased variability associated with the between-subjects nature of the comparison. Any differences should be associated with inter-task “set” differences. Thus, early, prestimulus differences could be reflected in the task comparisons.

Method

Participants

Fifty-one undergraduates (32 females) at the University of Florida participated in this experiment. Additionally, 7 undergraduates participated as pilot participants. Participants were randomly assigned to the two experimental groups. Participants received credit toward an introductory psychology course requirement or a nominal payment. Of the 51 participants who began the experiment, one failed to return for the test phase so neither behavioral nor EEG data were available for that participant. Two other participants had too few (< 10) incorrect responses to the memory test portion to permit construction of reliable waveforms. Finally, of the remaining 48 participants, various technical and signal-to-noise problems prevented analysis of another 13 EEG datasets.

Materials and Apparatus

Stimulus display and response recording

The study phase portion of the experiment was conducted under the same conditions and in the same location as the first experiment. The recognition phase (during which EEG was not recorded), which was held about 24 hours after completion of the study phase, was held in a brightly lit room not used for EEG recording. The recognition phase of Experiment Two was delayed after pilot testing indicated that there would be too few misses for item recognition to obtain interpretable ERPs in that condition. The same computer program used to display the material in Experiment 1 was used to display material in Experiment 2.

EEG recording

EEG recording was accomplished using the same parameters as in Experiment 1.

Stimulus materials

The study phase list from the first experiment was used to create a pair of study phase lists for the current experiment. The 160 object-location pairs were divided into 2 80-pair lists, each list serving, in one case, as study phase items and test phase foils, and, in the other case, as test phase foils and study phase items, respectively. All of the object-location pairs were separated to create two pairs of test phase lists (Objects/Locations) with each participant being shown an object list and its corresponding location list.

Design

The design for the study phase was a single factor (Bound, Separate) between-participants design. During the test phase, all participants were given item recognition tasks in which items were presented at the same rate as during Experiment 1. However, participants were required to respond “Old” or “New” (with same mouse press arrangement in Experiment 1) to each item, rather than following each pair. In addition, confidence ratings were obtained following each “Old/New” response. At the completion of the first 160 object or location recognition test, participants took the remaining (object or location) recognition test. Upon concluding the recognition test, participants completed a 32-item questionnaire (VVIQ-R; McKelvie, 2001) on the vividness of their visual imagery experiences.

Procedure

The study phase procedure was as described for Experiment 1 except that the participants were shown only one half of the object-location pairs. The remaining 80 pairs served as foils in the item recognition tests. Participants were reminded that they would return to the lab approximately 24 hours after completing the study phase to take a memory test and complete a questionnaire on mental imagery.

As in Experiment 1, the study phase, and each trial, commenced with a fixation cross, displayed for 300 ms, followed by a 700 ms post-fixation interval during which the screen was blank. Following the post-fixation interval, participants viewed words, presented singly in 28-point Arial font, each displayed for 500 ms with a 2500 ms interstimulus interval (ISI). Following the second word ISI, the ratings buttons were displayed until the participant selected one. At the end of 80 trials, the program stopped.

The experimenter then disconnected the participant from the EEG equipment, confirmed the following day's appointment, and dismissed the participant.

On the following day, the timing and appearance of stimulus items in the test phase was similar their presentation in the study phase; viz, a fixation cross, and an object, or a location, word were presented. However, the interstimulus interval between object and location words was reduced to 1500 ms and participants were shown either a list or 160 object words followed by a list of 160 location words or vice versa. List order, task and stimulus set was counterbalanced between subjects. Participants in both conditions (Bound/Separate) were instructed to indicate, using the left mouse button for affirmative responses and the right mouse button for negative responses, whether the word had been shown earlier (yes – left mouse button) or whether the word consisted of an object or location that had not been shown earlier (no – right mouse button). Participants were instructed to make these responses as quickly as possible due to the measurement of response times. Following the old-new mouse presses, the monitor displayed a three-choice alternative confidence rating (“Very confident,” “Somewhat confident,” “Just guessing”) to which participants were instructed to respond. Participants

were instructed to indicate the confidence with which they made their previous “old-new” responses.

Results

Behavioral Data

As displayed in Figure 1, in contrast to Experiment 1, in which large effects of the Task manipulation were observed, whether participants processed pairs under Bound (hits: $M = 57.3$, $SE = 3.21$; false alarms: $M = 23.7$, $SE = 4.25$) or Separate (hits: $M = 55.9$, $SE = 2.74$; false alarms: $M = 21.3$, $SE = 3.45$) imagery instructions had no impact on the probability of subsequent recognition of either objects or locations. On the other hand there was a large test effect. That is, collapsed across task, location words (hits: $M = 51.7$, $SE = 3.26$; false alarms: $M = 25.8$, $SE = 3.78$) were less well remembered than object words (hits: $M = 61.5$, $SE = 2.69$; false alarms: $M = 19.2$, $SE = 3.93$).

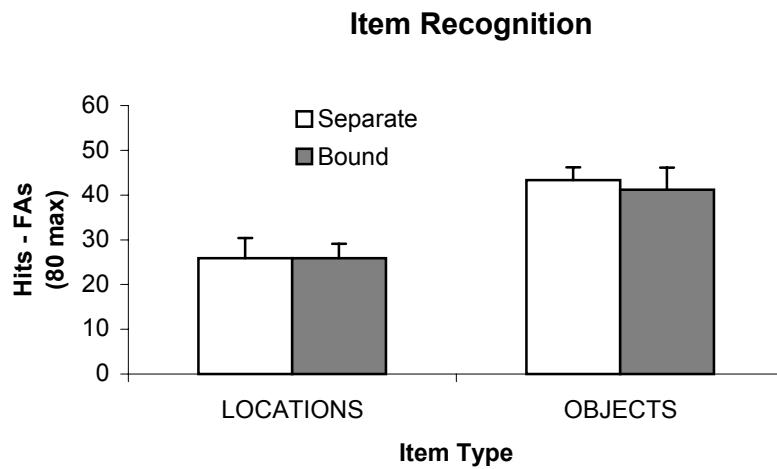


Figure 3-1. Behavioral performance in Experiment 2 (hits – false alarms) compared between the two encoding groups (Bound vs. Separate) and test type (Location vs. Object).

Furthermore, there was no impact on overall item recognition of whether participants were first given the object word or location word test. Likewise, as expected, there was no difference in recognition performance for the two stimulus sets.

EEG Data

ERP waveforms

ERPs elicited by word pairs in the study phase were, as noted, computed on the basis of participants' responses on the subsequent object recognition test. Data from the study phase were sorted as "hits or misses." As noted above, a large number of participants' data were excluded from analysis. Thirty-five participants (18 Bound/17 Separate) provided data for the analyses described below. Each participant's averaged data were then averaged with other participants' averaged data to calculate grand averaged data for each class.

ERPs to the Bound condition from the 13 scalp electrode sites are presented in Figure 3-2 below. As in the first experiment, over the course of the 6200 ms interval, discernible evoked responses to the onset of the first and second words (N100, P200, N400) are apparent at most sites across both conditions. Importantly, there are strong similarities between the waveforms generated by the participants in the Bound condition in Experiment 1 and those in the Bound condition in Experiment 2. These similarities are most apparent in the positive slow wave from 1200 ms to 3000 ms in the frontopolar sites, as well as a corresponding negative slow wave during the same interval at the Cz electrode. Thus, and to maintain consistent analysis across the two experiments, the same time windows were used for analysis in the second experiment as in the first experiment.

In the right hemisphere, the waveforms for hits and misses are nearly indistinguishable. Small differences, with remembered items being more positive than

forgotten items, appear in the prestimulus interval at FT7, as well as immediately preceding the onset of the second word at frontal sites (Fp1, Fp2, F3). Other differences appear in the region of the N400 to the second word at FT7. One difference that is similar to the Dm effects observed in Experiment 1 is found at Fp2 prior to the onset of the second word. In this case, forgotten items are more positive than remembered items. There are also late differences at F3 and FT7 with subsequently recognized items being more positive than forgotten items.

ERPs to the Separate condition from the 13 scalp electrode sites are presented in Figure 3-3 below. The waveforms again show marked deformations at standard component latencies (N100, P200, N400). As in the Bound condition, there is a notable positive-going slow wave between the first and second words at the frontal polar locations. At other locations, this time frame is either characterized by negative going activity or by little change in the overall polarity of the waveform. Unlike in the Bound condition, there is little difference in the waveforms between those to items later recognized and those subsequently missed, although some separation between hits and misses is noted beginning about 900 ms after the onset of the first word at Fp1.

The correct responses to old items in the Bound and Separate conditions are compared in Figure 3-4. Although collected from two different groups of participants under two different task instructions, the waveforms track each other closely, especially at posterior electrode sites. There appear to be differences, however, between the Separate and Bound groups, and these differences seem to be larger in the left hemisphere than in the right hemisphere and more pronounced at the anterior, than at the posterior, electrode sites.

Statistical analysis of waveforms

As in the first experiment, mean differences in EEG amplitudes during the study phase were conducted by running, for each condition (Bound and Separate), an analysis of variance (ANOVA) on the ten “windows” identified in Experiment 1 that comprised the total 6200 ms trial interval. The ANOVAs tested the same 3 factors (Performance: Hit/Miss; Hemisphere: Left/Right; Anterior-Posterior (“AntPos”): as in Experiment 1. In addition, a third set of ANOVAs was run to compare the mean amplitudes produced by correct responses to old items between the Bound and Separate conditions in each window. Thus, this ANOVA was a 3 factor (Condition: Bound/Separate; Hemisphere: Left/Right; Anterior-Posterior: 6 levels of electrode site), $2 \times 2 \times 6$, mixed design. The Greenhouse-Geisser correction (ϵ) was applied for violations of the assumptions of sphericity for comparisons involving two or more degrees of freedom.

Bound condition

Although there were no significant main effects of Performance or interactions between Performance and either AntPos or Hemisphere across any of the intervals, marginal effects were observed in the interval immediately preceding the onset of the second word (-400 – 0 ms) (Perf x Hemisphere: $F(1,17) = 4.349$, $p = .052$, $\epsilon = 1.00$ and early in the second word interval (0 - 300 ms), Perf: $F(1,17) = 4.326$, $p = .053$, $\epsilon = 1.00$. Neither the Perf x. AntPos, nor Perf x. AntPos, x Hemisphere interactions were significant (all p 's $> .05$).

Separate condition

The Separate condition showed no effects related to task performance (Perf, Perf x Hemisphere, Perf x AntPos, Perf x Hemisphere x AntPos: all p 's $> .10$).

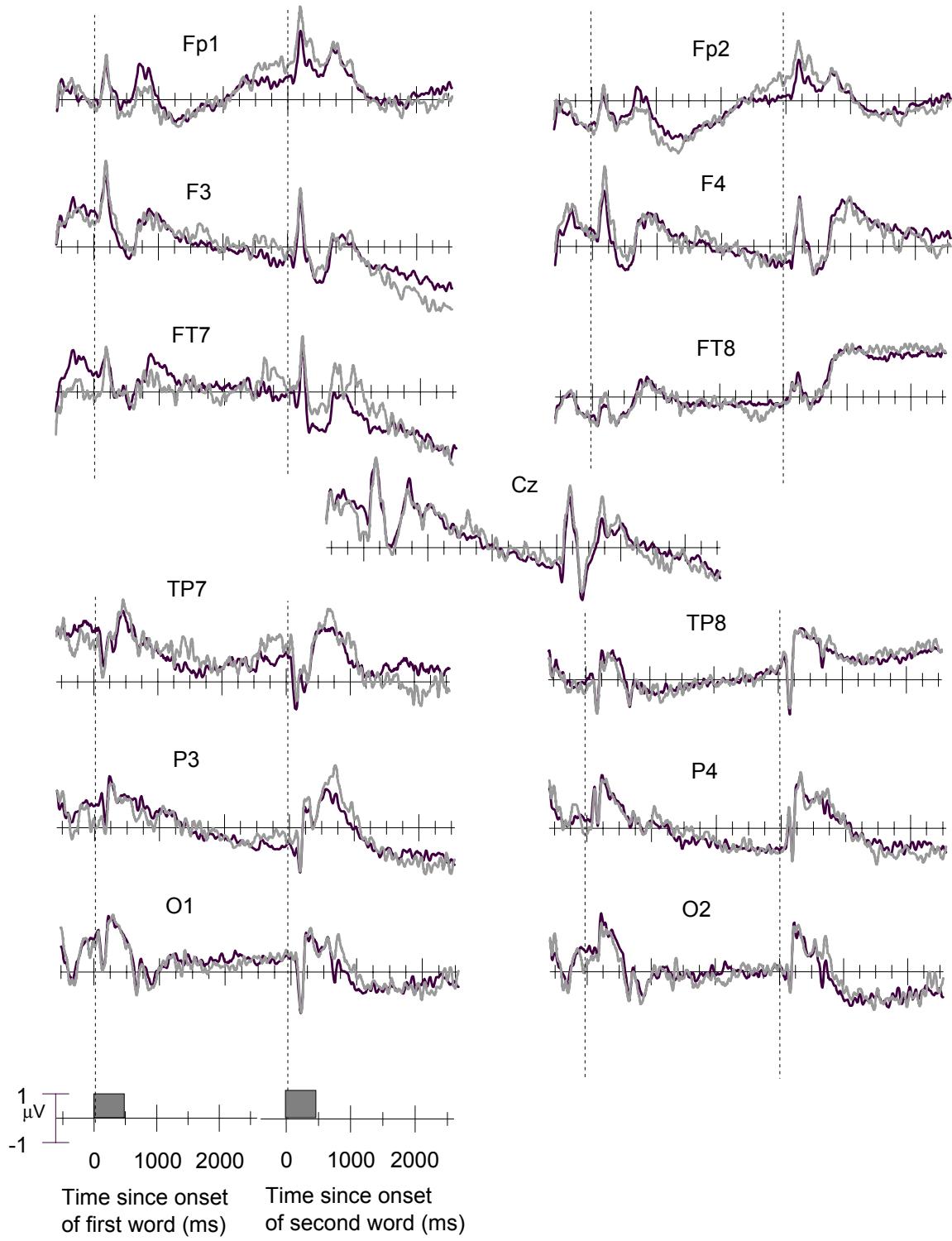


Figure 3-2. ERPs to two words during study phase during test in Experiment 2, Bound Encoding group. Bars indicate onset and offset times of the words. Black waveform is for first words (items: people, animals, objects) later correctly recognized as studied; grey waveform is for words later missed.

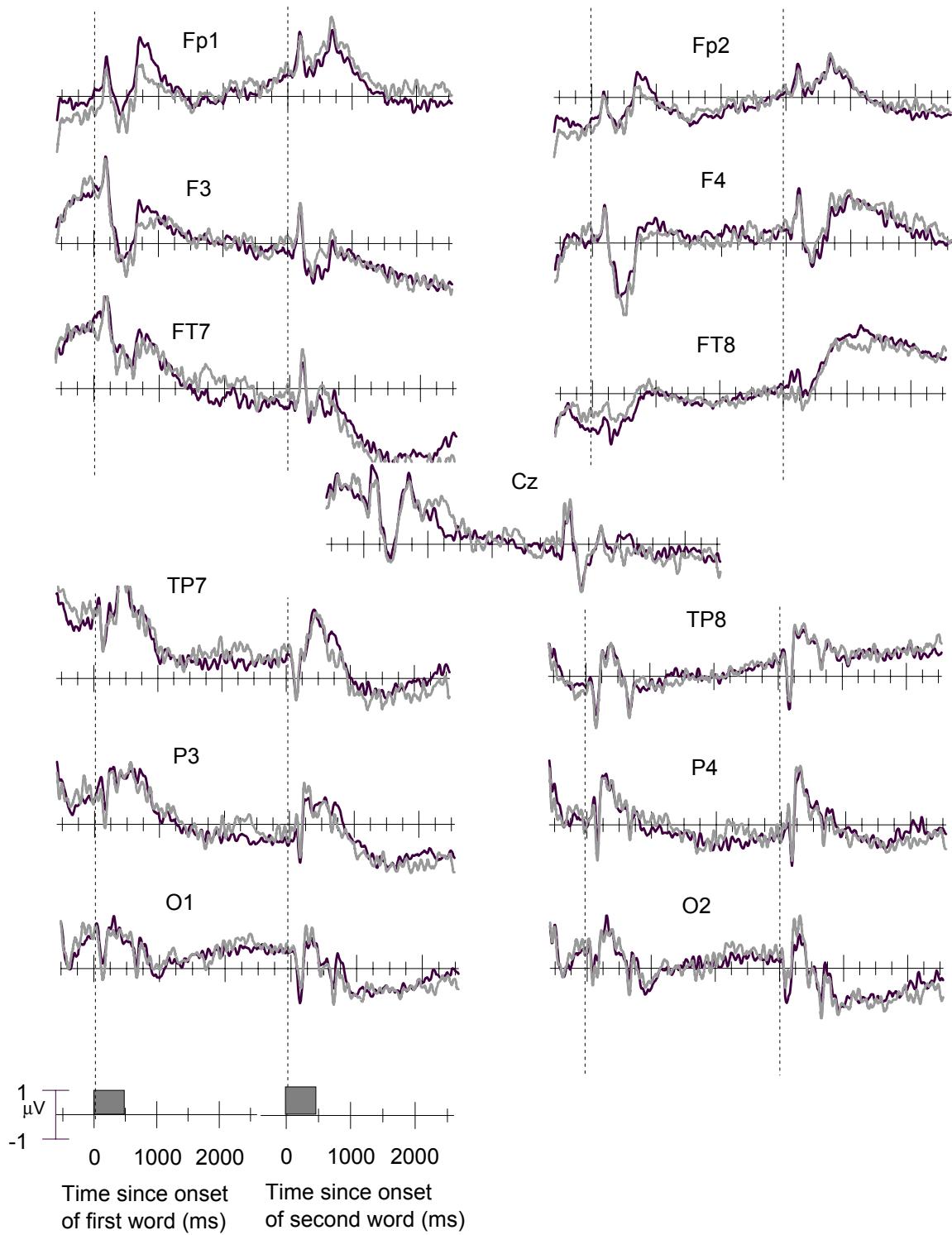


Figure 3-3. ERPs to two words during study phase during test in Experiment 2, Separate Encoding group. Bars indicate onset and offset times of the words. Black waveform is for first words (actors and objects) later correctly recognized as studied; grey waveform is for words later missed.

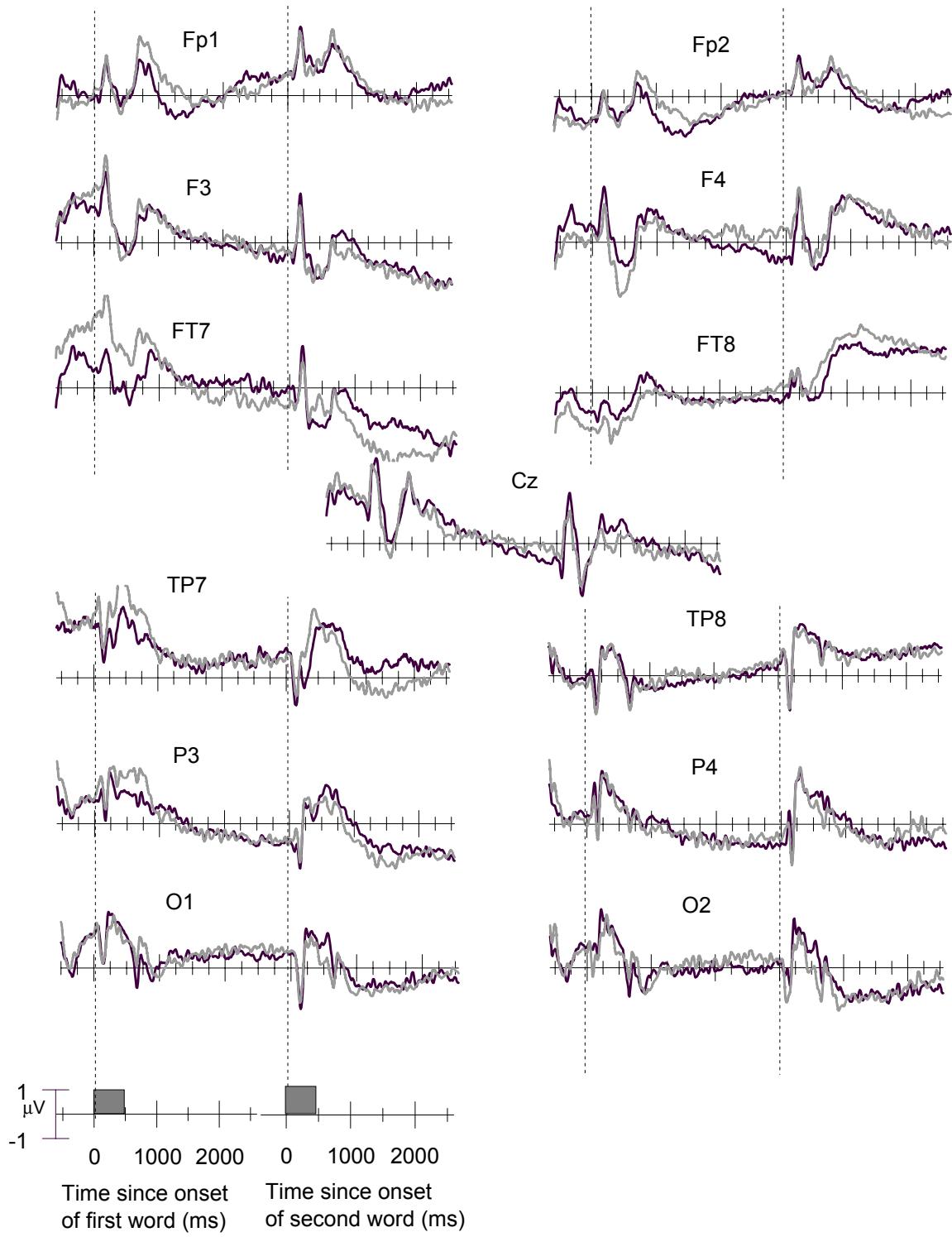


Figure 3-4. ERPs to two words during study phase later shown and correctly recognized as intact pairs during test in Experiment 2. Bars indicate onset and offset times of the words. Black waveform is for the Bound Encoding group; Grey waveform is for the Separate Encoding group

Bound vs. separate analysis

The third analysis consisted of comparing the mean differences between study pairs that yielded subsequent correct recognition of objects, people or animals, at test, in each of the two conditions. Differences were identified near the onset of the first word (0 - 300 ms) (Task x Hemisphere: $F(1,33) = 7.164$, $p = .011$, Task x Hemisphere x AntPos

Table 3-1. Time Intervals in Experiment 2 during which Amplitude Differences were Significant

Interval	Factor			
	Perf	Perf x AntPos	Perf x Hem	Perf x Ant Pos x Hem
[w1] -600 - 0				
0 – 300			H	H
300 - 600				
600 - 1200				
1200 -2600				
[w2] -400 - 0			B	
0 – 300	B			H
300 - 600				
600 - 1200				
1200 – 2600				

Note. “B” = marginally significant Dm effects in Bound task, “H” = significant differences in Bound – Separate correct recognition (Hit) comparison. There were no significant Dm effects in Separate task. **Bold**: $.06 > p > .05$. For all comparisons, $\alpha = .05$.

$F(2.271, 74.935) = 3.216$, $p = .040$) and near the onset of the second word (0 -300) (Task x Hemisphere x AntPos: $F(2.655, 87.615) = 3.043$, $p = .039$).

Discussion

Behavioral measures of performance in the second experiment revealed that single item recognition, whether for the first or second word of a pair, is unaffected by whether those items are the subject of relational processing. The trace that is generated in the encoding phase by either relational or single-item processing is sufficient to produce comparable levels of single item recognition. Levels of item recognition varied, however, by the nature of the target. Location words were less well recognized than object words. Location words, however, were always presented following object words in the study phase so it cannot be determined whether the decrement in location word recognition is attributable solely to the type of stimulus, or whether order effects also contributed to their poorer recognition performance. It might be argued, however, that if order effects were responsible, in part, for the decrement in location recognition, it would suffer less in the Bound condition than in the Separate condition, by virtue of the order being less salient to the encoding. However, the Perf x Item interaction was non-significant, suggesting that its recognition decrement was due primarily to the difficulty in encoding the locations.

The pattern of subsequent memory effects was different from, and less extensive than, that found in Experiment 1. Although none of the comparisons reached significance in the Bound condition, the marginally significant comparisons (Table 3-1) are discussed below. The separation of hits and misses in the end of the first word interval (reflected in a marginally significant Task x Hemisphere interaction ($p = .053$)), is characterized by left, but not right-sided amplitudes for the “miss” responses being larger than “hit” responses. In fact, visual inspection of the waveforms suggests that the differences are driven by a deflection of the “miss” responses. Whether this characterization is accurate

is difficult to determine but it suggests that the separation between hits and misses in the Bound condition is associated with some processing, or failure to process, the first word late in the interval. This interpretation is further supported by the lack of differences in the correct recognition responses to old words presented in the Bound and Separate conditions at those corresponding intervals.

Although there were suggestions in the waveforms of the Separate condition of subsequent memory differences, especially over the left hemisphere frontal electrodes at about 1200 ms and again at about 2000 ms at central locations, none of the hit-miss comparisons at any of the intervals reached significance. Although we predicted that the Separate (as well as the Bound) condition would yield subsequent memory effects for item recognition, at least to the first word, there is a possible explanation as to why no effects were observed. First, Dm effects have been shown to be extraordinarily sensitive to task demands. Thus, Paller et al. have shown that, under certain conditions, cued recall produces large Dm effects while item recognition does not. Similarly, recognition responses classified as “Remembered” (according to Tulving’s scheme) are more likely to produce Dm effects than “Know” responses. Thus, correct recognition responses to previously viewed items in the current experiment are likely to have included some proportion of guesses, or at the very least, trials on which the relational encoding failed (and thus would have been “Misses” in the first experiment). Analysis of the confidence ratings that participants gave during the recognition test and sorting of the study phase ERPs into more confident versus less confident responses is more likely to yield Dm effects.

The nature of the item Dm effects observed in the Bound, but not the Separate, condition is open for speculation. Visual inspection of the waveforms suggests that the Bound and Separate hits closely resemble the misses in the Separate condition in the interval (-400 – 0 ms) during which subsequent memory differences were observed. As noted, the misses in the Bound condition show a significant positive deflection. It could be that some aspect of relational processing has a detrimental effect on item recognition. For example, it could be that, in the Bound, but not the Separate, condition, participants shifted their attention from the first word in preparation for the presentation and integration of the second word. If an incomplete trace of the first (object) word was established at the time of the shift, then the miss trials might be associated with effects not observed in either the hit trials in the Bound and Separate conditions or the miss trials in the Separate condition.

The subsequent memory differences observed in the next window (0 – 300 ms), again for the Bound but not the Separate condition, may reflect the operation of similar cognitive processes that support (or impair) item recognition but have no impact on paired recognition. Thus, for example, a premature shift of attention to the second (location) word, in the Bound but not the Separate condition, could be reflected in the impaired recognition of the object but not the pair.

While the nature of the Dm effects observed for the Bound, but not the Separate, condition can be speculated at, there were clear task related differences in the second experiment, the nature of which seem to be more apparent. Correctly recognized first words were associated with differences in ERPs for the Bound and the Separate conditions at two similar intervals over the course of the trial. That is, at the onset of each

word (600 ms and 3600 ms), the differences between amplitude means for the Task x AntPos x Hem conditions were significant. These differences are likely to reflect strategy differences between the two tasks, given that an object to be integrated with a location may be processed differently than one that will face no such demands. Likewise, upon presentation of a location, there are demand differences for how that location will be processed in the Bound and Separate conditions.

The second experiment revealed a unique pattern of subsequent memory effects associated with item recognition, differing from those identified in Experiment 1. In contrast to the Dms that accompany paired recognition, item recognition Dms were restricted to the first word. This makes perfect sense, since the Dms were conditionalized on recognition of the first word. Somewhat unexpectedly, however, the subsequent memory effects were present only in the Bound task, and the relative similarity of the waveforms between the Bound and Separate conditions suggests that those differences may reflect error-related processing in the Bound case that may have been related to the integrative task.

CHAPTER 4 GENERAL DISCUSSION

The cognitive and neural processes that underlie successful episodic memory encoding include the creation of a memory trace that encompasses both an item or event and its spatiotemporal context. Little is known, however, about the way in which an item and its context are linked at the time of their presentation. By carefully manipulating the encoding task and memory test type, and sorting, post-hoc, encoding trials by subsequent memory performance the two ERP experiments reported here represent a novel approach to examining the cognitive and neural correlates of episodic memory encoding. Using this approach, we identified what is, to our knowledge, a unique set of ERP subsequent memory effects. Most notably, these include a frontopolar, positive-going, slow-wave potential late after the presentation of the first word of a pair that is more negative for pairs later successfully recognized, following imagistic processing of concrete nouns in an integrative encoding task (Bound condition, Experiment 1). This effect makes clear that relational processing begins even prior to the onset of the second item (here, the spatiotemporal “context”) in a pair, and suggests that prefrontal areas play an important role in this processing.

Distinctive Aspects of the Present Approach

Many ERP studies of episodic encoding compare the neural activity and behavioral performance associated with one type of task or process with that in a second task or process. Some other ERP studies sort, on a post-hoc basis, encoding trials by subsequent memory performance to compare the neural responses during trials associated

with later successful memory performance with those associated with later unsuccessful memory performance. We have utilized both elements while maintaining tight control over the stimulus materials and tasks.

By analyzing encoding ERPs according to subsequent memory performance, we have avoided encoding manipulations such as levels of processing as a proxy for memory performance. Such manipulations putatively generate better or worse memory performance but invariably include errors in the deep condition trials and correct responses in the shallow condition trials. Moreover, by not using such a manipulation, we were able to manipulate, systematically, an encoding strategy that addresses directly the question in which we were interested – are there discernable neural and cognitive processes associated with binding objects and locations in episodic memory? Thus, cognitive and neural processes associated with item-context binding that lead to successful episodic memory were isolated in a pair of carefully controlled experiments. In addition to using a unique paradigm, our experiments carefully controlled both the stimulus materials and task parameters to make comparisons between conditions and experiments valid.

So, for example, while one group of participants in the first experiment generated and maintained isolated images of the items and locations, another group generated and maintained integrated images of the same item-location pairs following identical presentation parameters. Moreover, the two groups were tested with identical stimuli, using the same test methods and instructions. Likewise, the second experiment used the same stimulus materials, method and instruction as in the first experiment. The only difference between the two experiments was in the test phase. Moreover, we used unique

item-context pairs throughout, thereby avoiding the stimulus repetition effects that make working memory and source memory paradigms difficult to implement in the study of long-term memory encoding. Although unique face-name (Guo et al., 2005) or face-occupation (Yovel & Paller, 2004) pairs have been used to study relational encoding, given the controversy surrounding the special cognitive and neural mechanisms of face encoding and recognition, our paradigm is more generalizable than face encoding studies. Moreover, in contrast to the remaining associative encoding studies, our experiments specify the nature of the relational encoding to be performed. Thus, the nature of any processes associated with one task, but not the other, can be described more precisely.

Finally, our experiments uniquely yielded the ability to contrast ERPs to the first and second stimulus item in a relational encoding paradigm. This feature enabled us to pose an as-yet unasked question: Are there cognitive and neural processes engaged by the presentation of the first item of a pair that are to be relationally encoded that are preparatory to the presentation of the second item? This question, which seems fundamental to notions of relational encoding, has not been addressed in any ERP study of which we are aware. In sum, no other subsequent memory ERP study has provided the degree of control, or the possibilities for isolating the constituent elements of relational encoding as the current pair of experiments.

Memory-Related ERPs and Integrative Episodic Encoding

The pair of experiments yielded clear evidence of task and test-dependent ERP effects that were associated with subsequent memory performance. As predicted, these effects differed in timing and topography that depended on both the encoding instructions and the retrieval demands imposed by the type of memory test given. Consistent with our predictions, when memory was queried by paired recognition, the subsequent memory

effects showed significantly different patterns between the two tasks. As expected in the integrative encoding condition, these effects arose at frontal electrode sites; importantly, there were no hemispheric differences. Moreover, the Dm effects occurred in response to each word, suggesting that some kind of item-related processing contributes to relational encoding success. In addition, an unexpected, widespread effect was observed early in the second word interval. This effect may have signaled the allocation of cognitive resources in preparation for subsequent integrative activity. Alternatively, it may be a carry-over of the preparatory Dm observed late in the first-word interval (see Figure 2-1).

In contrast to the pattern of activity observed in connection with the integrative instructions, Dm effects associated with the Separate instructions were restricted to (a) a prestimulus hemispheric difference, and (b) a transient, widespread effect immediately before the onset of the second word. The prestimulus Dm, which has not been reported before, may be an important indicator of attentional or other cognitive “set” differences that contributed to paired recognition success. Likewise, the widespread, transient effect just prior to onset of the second word may reflect the allocation of necessary attentional resources that separates later remembered from later-forgotten pairs. Although it is tempting to interpret the long-duration differences to each word in the Bound condition to item processing, their absence in the Separate condition suggests that those effects were not merely indicators of item-only processing. Rather, they likely reflect some degree of processing of the item as, to the first word, a to-be-integrated stimulus feature. The comparable second word Dm may be associated with the integration of the location with the object. Thus, contrary to our strongest predictions about the differences between the two conditions, successful encoding in the Bound task was not simply successful

encoding in the Separate task with an integrative component added on. Inclusion of the integrative component changed the entire pattern of neurocognitive activity associated with subsequent correct paired recognition.

Although memory was tested by paired recognition in Experiment 1, the patterns of results could have been due to the contributions of relational processing, item-only processing, or both. Thus, we conducted a second experiment using an item recognition test to discriminate between relational encoding processes that support pair recognition and item encoding processes that support simple recognition. We predicted that there would be little difference between the processes underlying item recognition whether or not a relational encoding strategy was used. Thus, we expected the patterns of subsequent memory differences between the Bound and the Separate conditions to be very similar when memory was tested by item recognition. As in the first experiment, there was no overlap between the Dm effects associated with the Bound encoding and Separate encoding strategies. In fact, there were no significant subsequent memory effects at all in the Separate condition, and only two intervals showed marginal Dm effects in the Bound condition. This finding is consistent with findings that recollection and recall tasks are more likely to produce Dm effects than item recognition and it suggests that the Bound Dm effects represent item-specific encoding processes, rather than relational encoding effects. The timing of the marginal Dm effects in the Bound condition is also consistent with our predictions. Encoding trials were classified on subsequent recognition of the item (person, animal, object) word, which was always presented as the first word of the pair during each study trial. Thus, Dm effects would be expected in response to the first, rather than the second, word interval. The marginally significant effects at the

presentation of the second word may reflect spillover from the sustained processing of the first word at the end of the interval.

Overall, then, the study produced, in each condition and experiment, a pattern of ERP differences that were, largely, consistent with our predictions.

Comparisons to Previous Findings

While there is a scarcity of findings regarding the ERP correlates of item-context encoding, Kounios and colleagues (2001) found that fusion association, in which two concepts are fused together to form a qualitatively distinguishable third concept (e.g., computer + virus = computer virus), has distinct neural correlates from juxtapositional association, in which two concepts are associated by contiguity. Fusion association was distinguishable by activity in right prefrontal cortex following the second word and waveform differences between quickly and slowly retrieved word pair orders at test at bilateral frontotemporal sites from 200 ms to 3000 ms after the onset of the second word.

While theoretical and methodological differences between Kounios and colleagues' work and the present study make direct comparisons difficult, it is worth noting that Kounios claimed that the difference in topography, timing and polarity between juxtapositional and fusion effects supported the idea that the two different cognitive processes are engaged by the different tasks. Likewise, in the current study, timing and topography differences between the effects found for encoding in the Bound condition and those found for Separate encoding, as classified by paired recognition performance support the idea that the two types of encoding recruit different cognitive processes. This claim is further buttressed by the finding that these effects differ from the Bound and Separate encoding effects that underlies item memory.

Of the ERP findings in the study, perhaps none is more striking than the pair of Dm effects that occur in similar, long (1400 ms) intervals following the presentation of the first and second words in the Bound, but not Separate, encoding task when trials are classified by performance on the paired recognition test. These effects, which have a frontal topography, differ from other observed frontal effects in associative memory encoding in two ways.

First, the effects in the interval following the first word ride on a positive-going slow wave beginning around 1400 ms after word onset. While we could not identify any studies other than Kounios and colleagues' (2001) that use a sequential S1-S2 word presentation paradigm in recognition memory, the positive-going nature of the slow wave, in contrast to the reversal (negative-going slow wave) at more posterior electrode sites is consistent with sustained positivity at frontopolar sites in other studies (Duarte et al., 2004; Mangels et al., 2001). As noted above, if our task is analogous to an S1-S2 task that typically elicits a negative-going slow wave, it is not surprising, perhaps, that the Fp sites yield positive-going slow change that persists until the onset of the second word. While the first word interval is followed by a frontal, positive-going slow wave, the second word is followed by a widespread negativity (with a notable exception at FT8). The Dm in this interval consists of the more typically observed pattern; subsequently recognized pairs are of greater positivity than subsequently missed items.

Second, the Dm for first words at frontopolar sites is of *negative* polarity (subsequent misses > subsequent hits). We have been able to identify only one other study (Guo et al., 2005) in which, at frontal sites, the amplitude of subsequently unrecognized items was more positive than that of subsequently recognized items.

Although it is unclear to what the negative Dm in Guo and colleagues' study can be attributed, it, too, was embedded in a sustained positive-going frontal wave (albeit only through the end of the 1s trial interval). Guo and colleagues' study involved participants intentionally encoding concurrently presented visually presented faces and auditorily presented names. The fact that face recognition Dms were significant in the later part of the interval and the name recognition Dms were significant only in the early interval suggests that the name and face were processed sequentially. Thus, it is possible that the negative Dm effects Guo and colleagues observed for name recognition reflect completion of the name processing and preparation for face name binding or maintenance of the name during face processing. This explanation, of course, is speculative and warrants further investigation.

The pattern of the Dms to the first and second word in the long interval is intriguing. Duarte and colleagues (2004), who found distinct subsequent memory effects for pictures subsequently classified as "remembered" or subsequently classified as "known" versus those that were missed, concluded that the sustained bilateral frontal activity associated with "remember" responses were attributable to "more extensive processing" than those later classified as "known." It could be that, in the Bound condition, participants were mentally "manipulating" or refining their images of the first word object in preparation for the required upcoming integration. No participants reported to us, however, any deliberate strategy in response to the first word. A better understanding of this first word, as well as its second word parallel, effect will be important in using ERPs to elucidate relational encoding.

The second pair of intriguing Dms are those that occurred, in the Bound condition conditionalized on paired recognition performance, to the second word; one a widespread, early (300 ms post-word 2 onset) effect, the other a late (1500 ms post-word 2 onset), frontal effect.

In the only experiment that we have identified that sequentially presented successive words for associative processing, and then measured ERPs to the second word, Kounios and colleagues (2001), found that participants who successfully fused word pairs into a unitary concept (e.g., computer + virus = “computer virus”) showed ERP differences according to whether they later quickly or slowly identified the order in which pairs were earlier presented. These differences persisted over the three-second interval following presentation of the second word. Interestingly, the initial differences (200-800 ms) were marked by activation in right prefrontal cortex. From 800 – 2100 ms following the second word, however, activation shifted to a region in left medial superior frontal cortex. In many respects, differences in experimental protocols between our experiments and Kounios and colleagues’ make comparisons between the two difficult. However, the fact that Kounios found a subsequent memory effects that persisted throughout a three second post word interval – and our results point to a pair of Dm effects that lasted nearly two seconds, is striking.

Likewise, in addition to an earlier set of subsequent memory effects, Mangels, Picton and Craik (2001) found sustained prefrontal positive and sustained posterior negative subsequent memory effects beginning at about 1000 ms after the onset of the word. They speculated that these effects reflected the interaction of a fronto-posterior network where the posterior portion of the network was responsible for sustained object

representation and the frontal part of the network, particularly at the Fp electrodes, playing a role in the elaborative processes that facilitate subsequent recollection and recognition. It is important to note that, similar to our studies, the Fp electrodes recorded a positive-going wave from about 1000 ms to the end of Mangel and colleagues' interval (2000 ms). Likewise, we found a positive slow wave at Fp sites from about 1000 ms following the first word until the first 200 ms following presentation of the second word. An important difference between Mangels' and our findings was that the slow wave in Mangels study was positive-going across most frontal electrodes (Fp, AF, F). The slow wave only became negative-going at posterior sites. In our experiments, the slow wave was positive-going only at Fp sites, and negative-going at other electrode locations. Another important difference, however, was in the polarity of the difference wave between Mangels' findings (positive at frontal sites, negative at posterior locations), and ours (negative at frontopolar sites).

Limitations and Future Directions

While the results from the experiments presented are unique and contribute to our understanding of the neurocognitive basis of relational encoding and long-term memory performance, there are aspects of the experimental design that limit the conclusions that can be drawn from them. First, although the design provides a unique amount of control over stimulus and task factors that could otherwise confound the results, the static item-location design fails to capture either the temporal or the dynamic aspects of episodic memory. As Craik (1989) notes, episodes, as described by Tulving (1984), consist of a series of events, which in turn consist of item/context pairs. Thus, by limiting the "episodes" here to single pairs, we have excluded participants' experience of ongoing events and the cognition that accompanies it. An initial foray into the dynamic aspect of

episodic encoding might include having participants generate dynamic images (i.e., visualize an ELEPHANT falling off of a CLIFF). Likewise, encoding activity for the temporal order of location-item pairs could be tested.

Second, by their design, the experiments allowed for the possibility of some overlap between the correct and incorrect response classes in that some trials in the correct response category (Experiment 1: Intact Correct; Experiment 2: Old – Old) may have been the result of low confidence guesses. Analysis of the confidence ratings in the test phase of Experiment 2 and resorting encoding trials into High and Medium Confidence correct responses and Low Confidence (Guessing) correct and incorrect trials would point to the degree of overlap and the contribution of guessing in the correct responses ERPs. No such confidence ratings were collected in the first experiment so defining the contribution of guessing trials to the correct responses would be more difficult.

Third, what role the ease with which pairs were capable of being imaged might have played is unclear. Although data regarding the ease of imagery were collected, these data have not been analyzed. It could be that, if these data were sorted into Easy and Difficult, they would correspond highly to correct and incorrect subsequent memory performance, suggesting a prominent role for the ease of imagery in encoding related memory effects. On the other hand, it might be that the greater cognitive effort expended in generating and maintaining difficult images would yield better memory performance.

Fourth, although low-density localization techniques (e.g., LORETA: Pascual-Marqui, Michel & Lehmann, 1994) are available, the use of a low-density (16 electrode) array made it difficult to attempt more serious source localization analysis. Nevertheless,

our use of traditional interval analyses and ANOVAs that included hemisphere and anterior-posterior groups as factors enabled us to generally identify regional activity. This regional activity was in accord with at least some previous findings where the source of neural activity has been identified using EEG localization (e.g., Kounios et al., 2001) and fMRI (e.g., Prabhakaran et al., 2000) techniques.

Fifth, keeping the encoding instructions and test type as between-subjects factors, one of the strengths of the design, also weakens the cross-task comparisons. The benefits of implementing the instruction and test type manipulation between subjects are clear. Participants are less likely to employ relational encoding strategies, even unintentionally, if they haven't engaged in them in a preceding study block. Likewise, if the test type were implemented as a within-subjects manipulation, participants would be likely to have received the benefit of item-retrieval in the paired recognition task (if it followed item recognition). Thus, the use of a between-subjects design for these factors largely keeps strategies and memory processes discrete from one another. However, the manipulations introduce a greater degree of variability than would be produced if they were manipulated within-subjects and, thus, tend to weaken the statistical comparison. It is possible that encoding comparisons would have produced more extensive differences than were observed. Moreover, manipulating test type as a within-subjects factor (if a way of keeping it from being confounded with retrieval practice could be ascertained) would facilitate the direct comparisons of the encoding processes that support the two memory retrieval types.

Finally, these data could be subjected to a coherence analysis, a technique that is being used increasingly in the study of memory encoding (e.g., Summerfield & Mangels,

2005; Weiss, Muller & Rappelsberger, 2000; Weiss & Rappelsberger, 2000). The essence of this type of analysis is to identify regions in which EEG bands from separate brain regions experience phase synchronization of neural oscillations over discrete temporal windows. This phase locking is considered a candidate code by which information is shared between spatially distinct brain areas (Summerfield & Mangels, 2005). While coherence analysis has been used to examine feature binding (Summerfield & Mangels, 2005) and perception (Engel, Fries & Singer, 2001), it seems to be a potentially important tool for investigating mechanisms that underlie the relational encoding that constitute item-context binding in episodic memory.

APPENDIX A
EXPERIMENT 1, STUDY PHASE WORD PAIRS

2.1 A FIREFLY/SIDEWALK /	WHEELBARROW/RINK /	PIG/WATERFALL /
1.2 A SURFER/STUDIO /	2.24 A COCKROACH/CARNIVAL	5.45 A RAKE/FARM /
3.3 O STEREO/MAILBOX /	/	7.46 O TAXI/ZOO /
2.4 O BUTTERFLY/BAKERY /	1.25 O KING/DUMP /	1.47 O BANDIT/CASINO /
2.5 I POSSUM/LOFT /	1.26 O DRUMMER/JUNGLE /	2.48 O GIRAFFE/CABINET /
2.6 I FLY/GLACIER /	3.27 O LAMP/TREE /	1.49 I MECHANIC/THICKET /
2.7 O TIGER/BARN /	7.28 O TRACTOR/DARKROOM /	2.50 O ANT/CATHEDRAL /
5.8 A PAINTBRUSH/RANCH /	2.29 A HIPPOPOTAMUS/GALLER	3.51 O COUCH/HILL /
2.9 O GORILLA/HOUSE /	Y /	5.52 O MOWER/CORNER /
1.10 A SOLDIER/PARTY /	7.30 A HELICOPTER/PHARMACY	4.53 I KNIFE/PYRAMID /
4.11 A BAYONET/WAREHOUSE /	/	2.54 A BIRD/MARKET /
1.12 A SKATER/STADIUM /	4.31 A ROCKET/CRATER /	6.55 O VIOLIN/WEDDING /
3.13 I DRESSER/MUSEUM /	2.32 I HORSE/BOX /	2.56 O OSTRICH/AMPHITHEATR
1.14 I SINGER/ROOF /	3.33 O TOILET/STEPS /	E /
3.15 O STOOL/RIDGE /	2.34 A MOUSE/KENNEL /	2.57 O BUFFALO/RESORT /
6.16 O TAMBOURINE/CLIFF /	1.35 A DETECTIVE/CAMP /	4.58 O BOMB/MOON /
2.17 I FROG/BILLBOARD /	8.36 A DOLLHOUSE/DRIVE-IN	2.59 O DUCK/HIGHWAY /
1.18 O LUMBERJACK/AVALANCH	/	1.60 A BARTENDER/VALLEY /
E /	7.37 O SUBMARINE/AIRPORT /	1.61 I DANCER/CAFÉ /
3.19 O CRIB/OFFICE /	1.38 I HIKER/BANK /	2.62 I COW/MORGUE /
2.20 O GRASSHOPPER/PENTHOU	7.39 O AIRPLANE/REEF /	2.63 A SEAL/BATHROOM /
SE /	2.40 I OWL/RAVINE /	4.64 O ROPE/CONVENTION /
1.21 I FIREMAN/BAR /	8.41 O BUBBLES/DISCO /	4.65 O CANNON/CABIN /
2.22 O TURTLE/FIREPLACE /	1.42 O DOORMAN/PLANTATION	7.66 I SKATES/TORNADO /
5.23 I	/	2.67 O
	5.43 I PENCIL/MANSION /	
	2.44 A	

OX/CHAPEL /	TOUCAN/DRIVEWAY /	DOLL/DORMITORY /
1.68 O	1.95 I	1.122 O
SWIMMER/HAYLOFT /	SAILOR/ATTIC /	BOY/SWAMP /
1.69 A	1.96 I	1.123 O
SLAVE/DESERT /	GYMNAST/PATH /	SKIER/APARTMENT /
8.70 O	1.97 O	5.124 A
ROBOT/RIVER /	DENTIST/TOMB /	LADDER/SNOWSTORM /
1.71 A	2.98 A	2.125 A
EXPLORER/TOWER /	LEOPARD/SKYSCRAPER	ANTELOPE/PLAYGROUND
5.72 A	/	/
SHOVEL/DOORWAY /	2.99 A	2.126 O
8.73 O	BEAR/BEDROOM /	CHICKEN/CANYON /
GLOVE/EARTHQUAKE /	1.100 A	3.127 O
1.74 O	CARPENTER/DUSK /	CHAIR/CITY /
BAKER/DAM /	5.101 O	1.128 A
2.75 O	PLANE/CELLAR /	CONDUCTOR/CLOUD /
CHIMPANZEE/ICEBERG /	4.102 A	2.129 O
2.76 A	ARROW/PLAYHOUSE /	CRAB/ALLEY /
HEDGEHOG/THUNDERSTORM /	1.103 I	2.130 A
7.77 A	INMATE/CHIMNEY /	RACCOON/DAYBREAK /
TANK/CEMETERY /	1.104 O	5.131 O
5.78 O	MILKMAN/COFFIN /	VISE/HAILSTORM /
DRILL/ISLAND /	2.105 A	4.132 O
7.79 O	PORCUPINE/OUTHOUSE	PILLOW/PRAIRIE /
SCOOTER/LABORATORY /	/	2.133 O
4.80 A	1.106 O	SQUIRREL/IGLOO /
BOOK/GROCERY /	PROSTITUTE/MALL /	8.134 A
8.81 O	4.107 A	PUPPET/TENT /
HORSESHOE/CLOSET /	FORK/TUNNEL /	5.135 O
2.82 A	7.108 A	WRENCH/PORCH /
OCTOPUS/PARK /	BICYCLE/BALCONY /	8.136 I
4.83 A	2.109 O	BOOMERANG/CREVICE /
GUN/FENCE /	LADYBUG/FORT /	7.137 O
2.84 A	8.110 A	SURFBOARD/WINDOW /
MANATEE/NURSERY /	CRAYONS/SEWER /	8.138 A
1.85 A	2.111 A	SOFTBALL/RAMP /
CLOWN/KITCHEN /	GOAT/BASEMENT /	1.139 A
2.86 O	1.112 A	JUGGLER/HOTEL /
LIZARD/MEADOW /	ASTRONAUT/WELL /	3.140 O
1.87 A	3.113 A	RADIO/ELEVATOR /
MAGICIAN/TEPEE /	STOVE/DECK /	2.141 A
1.88 O	7.114 A	FERRET/LIBRARY /
MAID/MOUNTAIN /	TRUCK/QUARRY /	6.142 O
1.89 A	1.115 A	CLARINET/GYMNASIUM
NUN/CORRAL /	GIRL/VOLCANO /	/
2.90 O	2.116 A	2.143 A
WOLF/BOULDER /	PANDA/LAUNDRY /	SPIDER/CAGE /
7.91 A	1.117 O	3.144 O
STREETCAR/SUNSET /	BRIDE/SHOWER /	BED/FLOOD /
7.92 I	7.118 O	1.145 A
BALLOON/MOSQUE /	RICKshaw/UNIVERSITY	JUDGE/HOSPITAL /
5.93 O	/	1.146 O
TOOLBOX/COTTAGE /	3.119 A	GROOM/JAIL /
2.94 A	VASE/ESCALATOR /	1.147 O
	6.120 O	BRICKLAYER/VILLAGE
	FLUTE/FOREST /	/
	8.121 O	2.148 A

LION/HUT /	WHALE/SLAUGHTERHOUS	CYMBALS/LAKE /
6.149 A	E /	3.157 A
GUITAR/CREEK /	6.153 O	PICTURE/SCHOOL /
4.150 O	HARP/GARAGE /	4.158 O
SPEAR/FOG /	6.154 A	SWORD/CAVE /
5.151 O	ACCORDION/GEYSER /	1.159 O
SCREWS/CIRCUS /	5.155 O	COWBOY/HARBOR /
2.152 A	SANDPAPER/OCEAN /	2.160 O
	6.156 A	RAT/BEACH /

APPENDIX B
EXPERIMENT 1, PAIRED RECOGNITION TEST WORD PAIRS

2.1 A O	TURTLE/FIREPLACE /	DOORMAN/PLANTATION
FIREFLY/SIDEWALK /	5.23 I O	/
1.2 A O	WHEELBARROW/RINK /	5.43 I O
SURFER/STUDIO /	2.24 A O	PENCIL/MANSION /
3.3 O O	COCKROACH/CARNIVAL	2.44 A O
STEREO/MAILBOX /	/	PIG/WATERFALL /
2.4 O O	1.25 O O	5.45 A O
BUTTERFLY/BAKERY /	KING/DUMP /	RAKE/FARM /
2.5 I O	1.26 O O	7.46 O O
OPOSSUM/LOFT /	DRUMMER/JUNGLE /	TAXI/ZOO /
2.6 I O	3.27 O O	1.47 O O
FLY/GLACIER /	LAMP/TREE /	BANDIT/CASINO /
2.7 O O	7.28 O O	2.48 O O
TIGER/BARN /	TRACTOR/DARKROOM /	GIRAFFE/CABINET /
5.8 A O	2.29 A O	1.49 I O
PAINTBRUSH/RANCH /	HIPPOPOTAMUS/GALLER	MECHANIC/THICKET /
2.9 O O	Y /	2.50 O O
GORILLA/HOUSE /	7.30 A O	ANT/CATHEDRAL /
1.10 A O	HELICOPTER/PHARMACY	3.51 O O
SOLDIER/PARTY /	/	COUCH/HILL /
4.11 A O	4.31 A O	5.52 O O
BAYONET/WAREHOUSE /	ROCKET/CRATER /	MOWER/CORNER /
1.12 A O	2.32 I O	4.53 I O
SKATER/STADIUM /	HORSE/BOX /	KNIFE/PYRAMID /
3.13 I O	3.33 O O	2.54 A O
DRESSER/MUSEUM /	TOILET/STEPS /	BIRD/MARKET /
1.14 I O	2.34 A O	6.55 O O
SINGER/ROOF /	MOUSE/KENNEL /	VIOLIN/WEDDING /
3.15 O O	1.35 A O	2.56 O O
STOOL/RIDGE /	DETECTIVE/CAMP /	OSTRICH/AMPHITHEATR
6.16 O O	8.36 A O	E /
TAMBOURINE/CLIFF /	DOLLHOUSE/DRIVE-IN	2.57 O O
2.17 I O	/	BUFFALO/RESORT /
FROG/BILLBOARD /	7.37 O O	4.58 O O
1.18 O O	SUBMARINE/AIRPORT /	BOMB/MOON /
LUMBERJACK/avalanch	1.38 I O	2.59 O O
E /	HIKER/BANK /	DUCK/HIGHWAY /
3.19 O O	7.39 O O	1.60 A O
CRIB/OFFICE /	AIRPLANE/REEF /	BARTENDER/VALLEY /
2.20 O O	2.40 I O	1.61 I O
GRASSHOPPER/PENTHOU	OWL/RAVINE /	DANCER/CAFE /
SE /	8.41 O O	2.62 I O
1.21 I O	BUBBLES/DISCO /	COW/MORGUE /
FIREMAN/BAR /	1.42 O O	2.63 A O
2.22 O O		SEAL/BATHROOM /

4.64 O O	WOLF/DORMITORY /	GIRL/BEACH /
ROPE/CONVENTION /	7.91 O N	2.118 O N
4.65 O O	STREETCAR/ELEVATOR	PANDA/VILLAGE /
CANNON/CABIN /	/	1.119 A N
7.66 I O	7.92 O N	BRIDE/RAMP /
SKATES/TORNADO /	BALLOON/IGLOO /	3.120 O N
2.67 O O	1.93 O N	VASE/MALL /
OX/CHAPEL /	LADYBUG/SUNSET /	6.121 A N
1.68 O O	5.94 A N	FLUTE/KITCHEN /
SWIMMER/HAYLOFT /	TOOLBOX/HOSPITAL /	8.122 O N
1.69 A O	2.95 O N	DOLL/JAIL /
SLAVE/DESERT /	TOUCAN/CITY /	1.123 A N
8.70 O O	7.96 A N	BOY/LIBRARY /
ROBOT/RIVER /	RICKSHAW/ESCALATOR	1.124 O N
1.71 A O	/	SKIER/PORCH /
EXPLORER/TOWER /	1.97 O N	5.125 O N
5.72 A O	SAILOR/CELLAR /	LADDER/OCEAN /
SHOVEL/DOORWAY /	1.98 A N	2.126 A N
8.73 O O	GYMNAST/VOLCANO /	ANTELOPE/NURSERY /
GLOVE/EARTHQUAKE /	1.99 A N	1.127 O N
1.74 O O	DENTIST/PLAYGROUND	CONDUCTOR/CAVE /
BAKER/DAM /	/	2.128 O N
2.75 O O	2.100 O N	CRAB/FOREST /
CHIMPANZEE/ICEBERG	LEOPARD/FLOOD /	2.129 A N
/	2.101 A N	RACCOON/DRIVEWAY /
2.76 A O	BEAR/OUTHOUSE /	5.130 A N
HEDGEHOG/THUNDERSTORM /	1.102 O N	VISE/DUSK /
7.77 A O	CARPENTER/FORT /	4.131 A N
TANK/CEMETERY /	5.103 A N	PILLOW/QUARRY /
5.78 O O	PLANE/CREEK /	3.132 A N
DRILL/ISLAND /	4.104 I N	CHAIR/FENCE /
7.79 O O	ARROW/CREVICE /	8.133 A N
SCOOTER/LABORATORY	1.105 O N	PUPPET/SLAUGHTERHOUSE /
/	INMATE/BOULDER /	5.134 A N
4.80 A O	1.106 O N	WRENCH/TUNNEL /
BOOK/GROCERY /	MILKMAN/APARTMENT /	8.135 I N
8.81 A N	5.107 O N	BOOMERANG/MOSQUE /
HORSESHOE/LAKE /	BED/FOG /	7.136 O N
2.82 I N	2.108 O N	SURFBOARD/MEADOW /
OCTOPUS/ATTIC /	PORCUPINE/CIRCUS /	8.137 O N
4.83 A N	1.109 O N	SOFTBALL/WINDOW /
GUN/SCHOOL /	PROSTITUTE/GARAGE /	1.138 O N
2.84 A N	4.110 A N	JUGGLER/CLOSET /
MANATEE/SNOWSTORM /	FORK/TENT /	3.139 A N
1.85 O N	7.111 A N	RADIO/CAGE /
CLOWN/COFFIN /	BICYCLE/LAUNDRY /	2.140 A N
2.86 O N	8.112 A N	FERRET/CORRAL /
LIZARD/MOUNTAIN /	CRAYONS/BASEMENT /	6.141 O N
1.87 A N	2.113 O N	CLARINET/CANYON /
MAGICIAN/SKYSCRAPER	GOAT/SWAMP /	2.142 A N
/	3.114 A N	SPIDER/BALCONY /
1.88 A N	STOVE/TEPEE /	3.143 A N
MAID/SEWER /	2.115 O N	ASTRONAUT/PLAYHOUSE /
1.89 A N	CHICKEN/HAILSTORM /	1.144 O N
NUN/HOTEL /	7.116 O N	JUDGE/COTTAGE /
2.90 O N	TRUCK/ALLEY /	
	1.117 O N	

1.145 A N GROOM/CLOUD /	5.151 A N SCREWS/BEDROOM /	CYMBALS/GYMNASIUM /
1.146 A N BRICKLAYER/PARK /	2.152 O N WHALE/SHOWER /	3.157 A N PICTURE/WELL /
2.147 A N LION/GEYSER /	6.153 O N HARP/UNIVERSITY /	4.158 O N SWORD/TOMB /
6.148 O N GUITAR/HARBOR /	6.154 A N ACCORDION/HUT /	1.159 I N COWBOY/PATH /
2.149 O N SQUIRREL/PRAIRIE /	5.155 A N SANDPAPER/DAYBREAK	2.160 A N RAT/DECK /
4.150 I N SPEAR/CHIMNEY /	/	
	6.156 O N	

APPENDIX C
EXPERIMENT 2, STUDY PHASE WORD PAIRS

2.1 A FIREFLY/SIDEWALK /	WHEELBARROW/RINK /	PIG/WATERFALL /
1.2 A SURFER/STUDIO /	2.24 A COCKROACH/CARNIVAL	5.45 A RAKE/FARM /
3.3 O STEREO/MAILBOX /	/	7.46 O TAXI/ZOO /
2.4 O BUTTERFLY/BAKERY /	1.25 O KING/DUMP /	1.47 O BANDIT/CASINO /
2.5 I POSSUM/LOFT /	1.26 O DRUMMER/JUNGLE /	2.48 O GIRAFFE/CABINET /
2.6 I FLY/GLACIER /	3.27 O LAMP/TREE /	1.49 I MECHANIC/THICKET /
2.7 O TIGER/BARN /	7.28 O TRACTOR/DARKROOM /	2.50 O ANT/CATHEDRAL /
5.8 A PAINTBRUSH/RANCH /	2.29 A HIPPOPOTAMUS/GALLER	3.51 O COUCH/HILL /
2.9 O GORILLA/HOUSE /	Y /	5.52 O MOWER/CORNER /
1.10 A SOLDIER/PARTY /	7.30 A HELICOPTER/PHARMACY	4.53 I KNIFE/PYRAMID /
4.11 A BAYONET/WAREHOUSE /	/	2.54 A BIRD/MARKET /
1.12 A SKATER/STADIUM /	4.31 A ROCKET/CRATER /	6.55 O VIOLIN/WEDDING /
3.13 I DRESSER/MUSEUM /	2.32 I HORSE/BOX /	2.56 O OSTRICH/AMPHITHEATR
1.14 I SINGER/ROOF /	3.33 O TOILET/STEPS /	E /
3.15 O STOOL/RIDGE /	2.34 A MOUSE/KENNEL /	2.57 O BUFFALO/RESORT /
6.16 O TAMBOURINE/CLIFF /	1.35 A DETECTIVE/CAMP /	4.58 O BOMB/MOON /
2.17 I FROG/BILLBOARD /	8.36 A DOLLHOUSE/DRIVE-IN	2.59 O DUCK/HIGHWAY /
1.18 O LUMBERJACK/AVALANCH	/	1.60 A BARTENDER/VALLEY /
E /	7.37 O SUBMARINE/AIRPORT /	1.61 I DANCER/CAFÉ /
3.19 O CRIB/OFFICE /	1.38 I HIKER/BANK /	2.62 I COW/MORGUE /
2.20 O GRASSHOPPER/PENTHOU	7.39 O AIRPLANE/REEF /	2.63 A SEAL/BATHROOM /
SE /	2.40 I OWL/RAVINE /	4.64 O ROPE/CONVENTION /
1.21 I FIREMAN/BAR /	8.41 O BUBBLES/DISCO /	4.65 O CANNON/CABIN /
2.22 O TURTLE/FIREPLACE /	1.42 O DOORMAN/PLANTATION	7.66 I SKATES/TORNADO /
5.23 I	/	1.68 O
	5.43 I PENCIL/MANSION /	
	2.44 A	

SWIMMER/HAYLOFT /	GLOVE/EARTHQUAKE /	CLOWN/KITCHEN /
1.69 A	1.74 O	1.87 A
SLAVE/DESERT /	BAKER/DAM /	MAGICIAN/TEPEE /
8.70 O	7.77 A	6.120 O
ROBOT/RIVER /	TANK/CEMETERY /	FLUTE/FOREST /
1.71 A	5.78 O	6.142 O
EXPLORER/TOWER /	DRILL/ISLAND /	CLARINET/GYMNASIUM
5.72 A	8.81 O	/
SHOVEL/DOORWAY /	HORSESHOE/CLOSET /	
8.73 O	1.85 A	

APPENDIX D
EXPERIMENT 2, OBJECT WORD TEST ITEMS

2.1 A O	COCKROACH /	2.48 O O
FIREFLY /	1.25 O O	GIRAFFE /
1.2 A O	KING /	1.49 I O
SURFER /	1.26 O O	MECHANIC /
3.3 O O	DRUMMER /	2.50 O O
STEREO /	3.27 O O	ANT /
2.4 O O	LAMP /	3.51 O O
BUTTERFLY /	7.28 O O	COUCH /
2.5 I O	TRACTOR /	5.52 O O
POSSUM /	2.29 A O	MOWER /
2.6 I O	HIPPOPOTAMUS /	4.53 I O
FLY /	7.30 A O	KNIFE /
2.7 O O	HELICOPTER /	2.54 A O
TIGER /	4.31 A O	BIRD /
5.8 A O	ROCKET /	6.55 O O
PAINTBRUSH /	2.32 I O	VIOLIN /
2.9 O O	HORSE /	2.56 O O
GORILLA /	3.33 O O	OSTRICH /
1.10 A O	TOILET /	2.57 O O
SOLDIER /	2.34 A O	BUFFALO /
4.11 A O	MOUSE /	4.58 O O
BAYONET /	1.35 A O	BOMB /
1.12 A O	DETECTIVE /	2.59 O O
SKATER /	8.36 A O	DUCK /
3.13 I O	DOLLHOUSE /	1.60 A O
DRESSER /	7.37 O O	BARTENDER /
1.14 I O	SUBMARINE /	1.61 I O
SINGER /	1.38 I O	DANCER /
3.15 O O	HIKER /	2.62 I O
STOOL /	7.39 O O	COW /
6.16 O O	AIRPLANE /	2.63 A O
TAMBOURINE /	2.40 I O	SEAL /
2.17 I O	OWL /	4.64 O O
FROG /	8.41 O O	ROPE /
1.18 O O	BUBBLES /	4.65 O O
LUMBERJACK /	1.42 O O	CANNON /
3.19 O O	DOORMAN /	7.66 I O
CRIB /	5.43 I O	SKATES /
2.20 O O	PENCIL /	1.67 O O
GRASSHOPPER /	2.44 A O	SWIMMER /
1.21 I O	PIG /	1.68 A O
FIREMAN /	5.45 A O	SLAVE /
2.22 O O	RAKE /	8.69 O O
TURTLE /	7.46 O O	ROBOT /
5.23 I O	TAXI /	1.70 A O
WHEELBARROW /	1.47 O O	EXPLORER /
2.24 A O	BANDIT /	5.71 A O

SHOVEL /	2.100 A N	CHAIR /
8.72 O O	LEOPARD /	1.129 A N
GLOVE /	2.101 A N	CONDUCTOR /
1.73 O O	BEAR /	2.130 O N
BAKER /	1.102 A N	CRAB /
7.74 A O	CARPENTER /	2.131 A N
TANK /	5.103 O N	RACCOON /
5.75 O O	PLANE /	5.132 O N
DRILL /	4.104 A N	VISE /
8.76 O O	ARROW /	4.133 O N
HORSESHOE /	1.105 I N	PILLOW /
1.77 A O	INMATE /	2.134 O N
CLOWN /	1.106 O N	SQUIRREL /
1.78 A O	MILKMAN /	8.135 A N
MAGICIAN /	2.107 A N	PUPPET /
6.79 O O	PORCUPINE /	5.136 O N
FLUTE /	1.108 O N	WRENCH /
6.80 O O	PROSTITUTE /	8.137 I N
CLARINET /	4.109 A N	BOOMERANG /
2.81 O N	FORK /	7.138 O N
OX /	7.110 A N	SURFBOARD /
2.82 O N	BICYCLE /	8.139 A N
CHIMPANZEE /	2.111 O N	SOFTBALL /
2.83 A N	LADYBUG /	1.140 A N
HEDGEHOG /	8.112 A N	JUGGLER /
7.84 O N	CRAYONS /	3.141 O N
SCOOTER /	2.113 A N	RADIO /
4.85 A N	GOAT /	2.142 A N
BOOK /	1.114 A N	FERRET /
2.86 A N	ASTRONAUT /	2.143 A N
OCTOPUS /	3.115 A N	SPIDER /
4.87 A N	STOVE /	3.144 O N
GUN /	7.116 A N	BED /
2.88 A N	TRUCK /	1.145 A N
MANATEE /	1.117 A N	JUDGE /
2.89 O N	GIRL /	1.146 O N
LIZARD /	2.118 A N	GROOM /
1.90 O N	PANDA /	1.147 O N
MAID /	1.119 O N	BRICKLAYER /
1.91 A N	BRIDE /	2.148 A N
NUN /	7.120 O N	LION /
2.92 O N	RICKshaw /	6.149 A N
WOLF /	3.121 A N	GUITAR /
7.93 A N	VASE /	4.150 O N
STREETCAR /	8.122 O N	SPEAR /
7.94 I N	DOLL /	5.151 O N
BALLOON /	1.123 O N	SCREWS /
5.95 O N	BOY /	2.152 A N
TOOLBOX /	1.124 O N	WHALE /
2.96 A N	SKIER /	6.153 O N
TOUCAN /	5.125 A N	HARP /
1.97 I N	LADDER /	6.154 A N
SAILOR /	2.126 A N	ACCORDION /
1.98 I N	ANTELOPE /	5.155 O N
GYMNAST /	2.127 O N	SANDPAPER /
1.99 O N	CHICKEN /	6.156 A N
DENTIST /	3.128 O N	CYMBALS /

3.157 A N
PICTURE /
4.158 O N
COWBOY /

2.160 O N
RAT /

APPENDIX E
EXPERIMENT 2, LOCATION WORD TEST ITEMS

2.1 A O	CARNIVAL /	2.48 O O
SIDEWALK /	1.25 O O	CABINET /
1.2 A O	DUMP /	1.49 I O
STUDIO /	1.26 O O	THICKET /
3.3 O O	JUNGLE /	2.5 O O
MAILBOX /	3.27 O O	CATHEDRAL /
2.4 O O	TREE /	3.51 O O
BAKERY /	7.28 O O	HILL /
2.5 I O	DARKROOM /	5.52 O O
LOFT /	2.29 A O	CORNER /
2.6 I O	GALLERY /	4.53 I O
GLACIER /	7.3 A O	PYRAMID /
2.7 O O	PHARMACY /	2.54 A O
BARN /	4.31 A O	MARKET /
5.8 A O	CRATER /	6.55 O O
RANCH /	2.32 I O	WEDDING /
2.9 O O	BOX /	2.56 O O
HOUSE /	3.33 O O	AMPHITHEATRE /
1.1 A O	STEPS /	2.57 O O
PARTY /	2.34 A O	RESORT /
4.11 A O	KENNEL /	4.58 O O
WAREHOUSE /	1.35 A O	MOON /
1.12 A O	CAMP /	2.59 O O
STADIUM /	8.36 A O	HIGHWAY /
3.13 I O	DRIVE-IN /	1.6 A O
MUSEUM /	7.37 O O	VALLEY /
1.14 I O	AIRPORT /	1.61 I O
ROOF /	1.38 I O	CAFÉ /
3.15 O O	BANK /	2.62 I O
RIDGE /	7.39 O O	MORGUE /
6.16 O O	REEF /	2.63 A O
CLIFF /	2.4 I O	BATHROOM /
2.17 I O	RAVINE /	4.64 O O
BILLBOARD /	8.41 O O	CONVENTION /
1.18 O O	DISCO /	4.65 O O
AVALANCHE /	1.42 O O	CABIN /
3.19 O O	PLANTATION /	7.66 I O
OFFICE /	5.43 I O	TORNADO /
2.2 O O	MANSION /	1.67 O O
PENTHOUSE /	2.44 A O	HAYLOFT /
1.21 I O	WATERFALL /	1.68 A O
BAR /	5.45 A O	DESERT /
2.22 O O	FARM /	8.69 O O
FIREPLACE /	7.46 O O	RIVER /
5.23 I O	ZOO /	1.7 A O
RINK /	1.47 O O	TOWER /
2.24 A O	CASINO /	5.71 A O

DOORWAY /	2.1 A N	CITY /
8.72 O O	SKYSCRAPER /	1.129 A N
EARTHQUAKE /	2.101 A N	CLOUD /
1.73 O O	BEDROOM /	2.13 O N
DAM /	1.102 A N	ALLEY /
7.74 A O	DUSK /	2.131 A N
CEMETERY /	5.103 O N	DAYBREAK /
5.75 O O	CELLAR /	5.132 O N
ISLAND /	4.104 A N	HAILSTORM /
8.76 O O	PLAYHOUSE /	4.133 O N
CLOSET /	1.105 I N	PRAIRIE /
1.77 A O	CHIMNEY /	2.134 O N
KITCHEN /	1.106 O N	IGLOO /
1.78 A O	COFFIN /	8.135 A N
TEPEE /	2.107 A N	TENT /
6.79 O O	OUTHOUSE /	5.136 O N
FOREST /	1.108 O N	PORCH /
6.8 O O	MALL /	8.137 I N
GYMNASIUM /	4.109 A N	CREVICE /
2.81 O N	TUNNEL /	7.138 O N
CHAPEL /	7.11 A N	WINDOW /
2.82 O N	BALCONY /	8.139 A N
ICEBERG /	2.111 O N	RAMP /
2.83 A N	FORT /	1.14 A N
THUNDERSTORM /	8.112 A N	HOTEL /
7.84 O N	SEWER /	3.141 O N
LABORATORY /	2.113 A N	ELEVATOR /
4.85 A N	BASEMENT /	2.142 A N
GROCERY /	1.114 A N	LIBRARY /
2.86 A N	WELL /	2.143 A N
PARK /	3.115 A N	CAGE /
4.87 A N	DECK /	3.144 O N
FENCE /	7.116 A N	FLOOD /
2.88 A N	QUARRY /	1.145 A N
NURSERY /	1.117 A N	HOSPITAL /
2.89 O N	VOLCANO /	1.146 O N
MEADOW /	2.118 A N	JAIL /
1.9 O N	LAUNDRY /	1.147 O N
MOUNTAIN /	1.119 O N	VILLAGE /
1.91 A N	SHOWER /	2.148 A N
CORRAL /	7.12 O N	HUT /
2.92 O N	UNIVERSITY /	6.149 A N
BOULDER /	3.121 A N	CREEK /
7.93 A N	ESCALATOR /	4.15 O N
SUNSET /	8.122 O N	FOG /
7.94 I N	DORMITORY /	5.151 O N
MOSQUE /	1.123 O N	CIRCUS /
5.95 O N	SWAMP /	2.152 A N
COTTAGE /	1.124 O N	SLAUGHTERHOUSE /
2.96 A N	APARTMENT /	6.153 O N
DRIVEWAY /	5.125 A N	GARAGE /
1.97 I N	SNOWSTORM /	6.154 A N
ATTIC /	2.126 A N	GEYSER /
1.98 I N	PLAYGROUND /	5.155 O N
PATH /	2.127 O N	OCEAN /
1.99 O N	CANYON /	6.156 A N
TOMB /	3.128 O N	LAKE /

3.157 A N
SCHOOL /
4.158 O N

CAVE /
1.159 O N
HARBOR /

2.16 O N
BEACH /

LIST OF REFERENCES

- Baddeley, A. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Sciences*, 11, 417-423.
- Baker, J. T., Sanders, A. L., Maccotta, L., & Buckner, R. L. (2001). Neural correlates of verbal memory encoding during semantic and structural processing tasks. *NeuroReport*, 12, 1251-1256.
- Bar, M., & Aminoff, E. (2003). Cortical analysis of visual context. *Neuron*, 38, 347-358.
- Battig, W. F., & Montague, W. E. (1969). Category norms for verbal items in 56 categories: A replication and extension of the Connecticut category norms. *Journal of Experimental Psychology*, 80, (3, pt. 2), 1-46.
- Bor, D., Duncan, J., Wiseman, R. J., & Owen, A. M. (2003). Encoding strategies dissociate prefrontal activity from working memory demand. *Neuron*, 37, 361-367.
- Bower, G.H. (1970). Imagery as a relational organizer in associative memory. *Journal of Verbal Learning and Verbal Behavior*, 9, 529-533.
- Brewer, J. B., Zhao, Z., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1998). Making memories: Brain activity that predicts how well visual experience will be remembered. *Science*, 281, 1185-1187.
- Buckner, R. L., Wheeler, M. E., & Sheridan, M. (2001). Encoding processes during retrieval tasks. *Journal of Cognitive Neuroscience*, 13, 406-415.
- Cabeza, R., & Nyberg, L. (2000). Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience*, 12, 1-47.
- Cansino, S., Maquet, P., Dolan, R. J., & Rugg, M. D. (2002). Brain activity underlying encoding and retrieval of source memory. *Cerebral Cortex*, 12, 1048-1056.
- Casasanto, D. J., Killgore, W. D. S., Maldjian, J. A., Glosser, G., Alsop, D. C., Cooke, A. M., Grossman, M., & Detre, J. A. (2002). Neural correlates of successful and unsuccessful verbal memory encoding. *Brain and Language*, 80, 287-295.

- Chalfonte, B. L., & Johnson, M. K. (1996). Feature memory and binding in young and older adults. *Memory & Cognition*, 24, 403-416.
- Clark, D., & Wagner, A. D. (2003). Assembling and encoding word representations: fMRI subsequent memory effects implicate a role for phonological control. *Neuropsychologia*, 41, 304-317.
- Craik, F. I. M. (1989). On the making of episodes. In H.L.Roediger III & F. I. M. Craik (Eds.), *Varieties of memory and consciousness: Essays in honour of Endel Tulving* (pp. 43-57). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Daselaar, S. M., Veltman, D. J., Rombouts, S. A. R. B., Raaijmakers, J. G. W., & Jonker, C. (2003). Neuroanatomical correlates of episodic encoding and retrieval in young and elderly subjects. *Brain*, 126, 43-56.
- Davachi, L., Maril, A., & Wagner, A. D. (2001). When keeping in mind supports later bringing to mind: Neural markers of phonological rehearsal predict subsequent remembering. *Journal of Cognitive Neuroscience*, 13, 1059-1070.
- Davachi, L., Mitchell, J. P., & Wagner, A. D. (2003). Multiple routes to memory: Distinct medial temporal lobe processes build item and source memories. *Proceedings of the National Academy of Sciences*, 100, 2157-2162.
- Davachi, L., & Wagner, A. D. (2002). Hippocampal contributions to episodic encoding: Insights from relational and item-based learning. *Journal of Neurophysiology*, 88, 982-990.
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134, 9-21.
- Duarte, A., Ranganath, C., Winward, L., Hayward, D., & Knight, R. T. (2004). Dissociable neural correlates in familiarity and recollection during the encoding and retrieval of pictures. *Cognitive Brain Research*, 18, 255-272.
- Engel, A. K., Fries, P., & Singer, W. (2001). Dynamic predictions: Oscillations and synchrony in top-down processing. *Nature Reviews Neuroscience*, 2, 704-716.
- Fabiani, M., & Donchin, E. (1995). Encoding process and memory organization: A model of the van Restorff effect. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 21, 224-240.
- Fabiani, M., Karis & Donchin, E. (1990). Effects of mnemonic strategy manipulation in a Von Restorff paradigm. *Electroencephalography and Clinical Neurophysiology*, 75, 22-35.

- Fabiani, M., Karis, D., & Donchin, E. (1986). P300 and recall in an incidental memory paradigm. *Psychophysiology*, 23, 298-308.
- Fernandez, G., Effern, A., Grunwald, T., Pezer, N., Lehnertz, K., Kampelmann, M., Van Roost, D., & Elger, C. E. (1999). Real-time tracking of memory formation in the human rhinal cortex and hippocampus. *Science*, 285, 1582-1585.
- Fernandez, G., Weyerts, H., Tendolkar, I., Smid, H. G. O. M., Scholz, M., & Heinze, H.-J. (1998). Event-related potentials of verbal encoding into episodic memory: Dissociation between the effects of subsequent memory performance and distinctiveness. *Psychophysiology*, 35, 709-720.
- Fletcher, P. C., Frith, C. D., & Rugg, M. D. (1997). The functional neuroanatomy of episodic memory. *Trends in Neurosciences*, 20, 213-218.
- Fletcher, P. C., & Henson, R. N. A. (2001). Frontal lobes and human memory: Insights from functional neuroimaging. *Brain*, 124, 849-881.
- Friedman, D. (1990). ERPs during continuous recognition for words. *Biological Psychology*, 30, 61-87.
- Friedman, D., Ritter, W., & Snodgrass, J. G. (1996). ERPs during study as a function of subsequent direct and indirect memory testing in young and old adults. *Cognitive Brain Research*, 4, 1-13.
- Friedman, D., & Trott, C. (2000). An event-related potential study of encoding in young and older adults. *Neuropsychologia*, 38, 542-557.
- Gonsalves, B., & Paller, K. A. (2000). Neural events that underlie remembering something that never happened. *Nature Neuroscience*, 3, 1316-1321.
- Guo, C., Voss, J. L., & Paller, K. A. (2005). Electrophysiological correlates of forming memories for faces, names, and face-name associations. *Cognitive Brain Research*, 22, 153-164.
- Guo, C., Zhu, Y., Ding, J., Fan, S., & Paller, K. A. (2004). An electrophysiological investigation of memory encoding, depth of processing, and word frequency in humans. *Neuroscience Letters*, 356, 79-82.
- Habib, R., Nyberg, L., & Tulving, E. (2003). Hemispheric asymmetries of memory: The HERA model revisited. *Trends in Cognitive Sciences*, 7, 241-245.
- Hasher, L., & Zacks, R. T. (1979). Automatic and effortful processes in memory. *Journal of Experimental Psychology: General*, 108, 356-388.

- Henkel, L. A., Johnson, M. K., & DeLeonardis, D. M. (1998). Aging and source monitoring: Cognitive processes and neuropsychological correlates. *Journal of Experimental Psychology: General*, 127, 251-268.
- Henson, R. N. A., Rugg, M. D., Shallice, T., Josephs, O., & Dolan, R. J. (1999). Recollection and familiarity in recognition memory: An event-related functional magnetic resonance imaging study. *Journal of Neuroscience*, 19, 3962-3972.
- Hunt, R. R., & Einstein, G. O. (1981). Relational and item specific information in memory. *Journal of Verbal Learning and Verbal Behavior*, 20, 497-514.
- Jackson, III, O., & Schacter, D. L. (2003). Encoding activity in anterior medial temporal lobe supports subsequent associative recognition. *Neuroimage*, 21, 456-462.
- Janata, P. (2001). Brain electrical activity evoked by mental formation of auditory expectations and images. *Brain Topography*, 13, 169-193.
- Johnson, M. K. (1992). MEM: Mechanisms of recollection. *Journal of Cognitive Neuroscience*, 4, 268-280.
- Johnson, M. K., & Hirst, W. (1993). MEM: Memory subsystems as processes. In A. Collins, S. Gathercole, M. Conway, & P. Morris (Eds.), *Theories of Memory* (pp. 241-286). Hillsdale, NJ: Erlbaum.
- Johnson, Jr., R. (1995). Event-related potential insights into the neurobiology of memory systems. In F. Boller & J. Grafman. *Handbook of Neuropsychology* (pp. 135-164). Amsterdam: Elsevier.
- Karis, D., Fabiani, M., & Donchin, E. (1984). P300 and memory: Individual differences in the Von Restorff effect. *Cognitive Psychology*, 16, 177-216.
- Kensinger, E. A., Clarke, R. J., & Corkin, S. (2003). What neural correlates underlie successful encoding and retrieval? A functional magnetic resonance imaging study using a divided attention paradigm. *Journal of Neuroscience*, 23, 2407-2415.
- Kirchoff, B. A., Wagner, A. D., Maril, A., & Stern, C. E. (2000). Prefrontal-temporal circuitry for episodic encoding and subsequent memory. *Journal of Neuroscience*, 20, 6173-6180.
- Kounios, J., Smith, R., Yang, W., Bachman, P., & D'Esposito, M. (2001). Cognitive association formation in human memory revealed by spatiotemporal brain imaging. *Neuron*, 29, 297-306.
- Lian, J., Goldstein, A., Donchin, E., & He, B. (2002). Cortical potential imaging of episodic memory encoding. *Brain Topography*, 15, 29-36.

- Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, 390, 279-281.
- Mangels, J. A., Picton, T. W., & Craik, F. I. M. (2001). Attention and successful episodic encoding: an event-related potential study. *Cognitive Brain Research*, 11, 77-95.
- Mayes, A. R. & Montaldi, D. (1999). The neuroimaging of long-term memory encoding processes. *Memory*, 7, 613-659.
- Mecklinger, A., & Muller, N. (1996). Dissociations in the processing of "what" and "where" information in working memory: An event-related potential analysis. *Journal of Cognitive Neuroscience*, 8, 453-473.
- Mitchell, K. J., Johnson, M. K., Raye, C. L., & D'Esposito, M. (2000a). fMRI evidence of age-related hippocampal dysfunction in feature binding in working memory. *Cognitive Brain Research*, 10, 197-206.
- Mitchell, K. J., Johnson, M. K., Raye, C. L., Mather, M., & D'Esposito, M. (2000b). Aging and reflective processes of working memory: Binding and test load deficits. *Psychology and Aging*, 15, 527-541.
- Neville, H. J., Kutas, M., Chesney, G., & Schmidt, A. L. (1986). Event-related brain potentials during initial encoding and recognition memory of congruous and incongruous words. *Journal of Memory and Language*, 25, 75-92.
- Nyberg, L. (2002). Levels of processing: A view from functional brain imaging. *Memory*, 10, 345-348.
- Nyberg, L., Cabeza, R., & Tulving, E. (1996). PET studies of encoding and retrieval: The HERA model. *Psychonomic Bulletin and Review*, 3, 135-148.
- Otten, L. J., Henson, R. N. A., & Rugg, M. D. (2001). Depth of processing effects on neural correlates of memory encoding: Relationship between findings from across- and within-task comparisons. *Brain*, 124, 399-412.
- Otten, L. J. & Rugg, M. D. (2001). Task-dependency of the neural correlates of episodic encoding as measured by fMRI. *Cerebral Cortex*, 11, 1150-1160.
- Paller, K. A., & Wagner, A. D. (2002). Observing the transformation of experience into memory. *Trends in Cognitive Sciences*, 6, 93-102.
- Pascual-Marqui, R. D., Michel, C. M. & Lehmann, D. (1994). Low resolution electromagnetic tomography: A new method for localizing electrical activity in the brain. *International Journal of Psychophysiology*, 18, 49-65.

- Prabhakaran, V., Narayanan, K., Zhao, Z., & Gabrieli, J. D. E. (2000). Integration of diverse information in working memory within the frontal lobe. *Nature Neuroscience*, 3, 85-90.
- Ranganath, C., Johnson, M. K., & D'Esposito, M. (2003). Prefrontal activity associated with working memory and episodic long-term memory. *Neuropsychologia*, 41, 378-389.
- Ranganath, C., Yonelinas, A. P., Cohen, M. X., Dy, C. J., Tom, S. M. D' Esposito, M. (2004). Dissociable correlates of recollection and familiarity within the medial temporal lobes. *Neuropsychologia*, 42, 2-13.
- Raye, C. L., Johnson, M. K., Mitchell, K. J., Reeder, J. A., & Greene, E. J. (2002). Neuroimaging a single thought: dorsolateral PFC activity associated with refreshing just-activated information. *Neuroimage*, 15, 447-453.
- Reber, P. J., Siwiec, R. M., Gitelman, D. R., Parrish, T. B., Mesulam, M. M., & Paller, K. A. (2002). Neural correlates of successful encoding identified using functional magnetic resonance imaging. *Journal of Neuroscience*, 22, 9541-9548.
- Rossi, S., Cappa, S. F., Babiloni, C., Pasqualetti, P., Miniussi, C., Carducci, F., Babiloni, F., & Rossini, P. M. (2001). Prefrontal cortex in long-term memory: an "interference" approach using magnetic stimulation. *Nature Neuroscience*, 4, 948-952.
- Rubin, D. C., & Friendly, M. (1986). Predicting which words get recalled: Measures of free recall, availability, goodness, emotionality and pronouncability for 925 nouns. *Memory and Cognition*, 14, 79-94.
- Rugg, M. D., & Allan, K. (2000). Event-related potential studies of memory. In E. Tulving & F. I. M. Craik (Eds.) *Oxford Handbook of Memory* (pp. 521-537). London: Oxford University Press
- Rypma, B., & D'Esposito, M. (2003). A subsequent-memory effect in dorsolateral prefrontal cortex. *Cognitive Brain Research*, 16, 162-166.
- Sanquist, T. F., Rohrbaugh, J. W., Syndulko, K., & Lindsley, D. B. (1980) Electrocortical signs of levels of processing: Perceptual analysis and recognition memory. *Psychophysiology*, 17, 568-576.
- Schacter, D. L (2001). *The Seven Sins of Memory: How the Mind Forgets and Remembers*. Boston, Houghton-Mifflin
- Schacter, D. L., & Wagner, A. D. (1999). Medial temporal lobe activations in fMRI and PET studies of encoding and retrieval. *Hippocampus*, 9, 7-24.

- Schott, B., Richardson-Klavehn, A., Heinze, H.-J., & Duzel, E. (2002). Perceptual priming versus explicit memory: Dissociable neural correlates at encoding. *Journal of Cognitive Neuroscience*, 14, 578-592.
- Smith, M. E. (1993). Neurophysiological manifestations of recollective experience during recognition memory judgments. *Journal of Cognitive Neuroscience*, 5, 1-13.
- Smith, M. E., & Halgren, E. (1989). Dissociation of recognition memory components following temporal lobe lesions. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 15, 50-60.
- Sommer, T., Rose, M., Weiller, C., & Buchel, C. (2005). Contributions of occipital, parietal and parahippocampal cortex to encoding of object-location associations. *Neuropsychologia*, 43, 732-743.
- Sperling, R., Chua, E., Cocchiarella, A., Rand-Giovanetti, E., Poldrack, R., Schacter, D. L., & Albert, M. (2003). Putting names to faces: Successful encoding of associative memories activates the anterior hippocampal formation. *Neuroimage*, 20, 1400-1410.
- Stark, C. E. L., & Okado, Y. (2003). Making memories without trying: medial temporal lobe activity associated with incidental memory formation during recognition. *Journal of Neuroscience*, 23, 6748-6753.
- Strange, B. A., Otten, L. J., Josephs, O., Rugg, M. D., & Dolan, R. J. (2002). Dissociable human perirhinal, hippocampal, and parahippocampal roles during verbal encoding. *Journal of Neuroscience*, 22, 523-528.
- Summerfield, C., & Mangels, J. A. (2005). Coherent theta-band EEG activity predicts item-context binding during encoding. *Neuroimage*, 24, 692-703.
- Tulving, E. (1984). Precis of elements of episodic memory. *Behavioral and Brain Sciences*, 7, 223-238.
- Tulving, E. (1985). Memory and consciousness. *Canadian Psychology*, 26, 1-12.
- Tulving, E., Kapur, S., Craik, F. I. M., Moscovitch, M., & Houle, S. (1994). Hemispheric encoding/retrieval asymmetry in episodic memory: Positron emission tomography findings. *Proceedings of the National Academy of Science*, 91, 2016-2020.
- Turriziani, P., Fadda, L., Caltagirone, C., & Carlesimo, G. A. (2004). Recognition memory for single items and for associations in amnesic patients. *Neuropsychologia*, 42, 426-433.

- Van Petten, C., & Senkfor, A. J. (1996). Memory for words and novel visual patterns: Repetition, recognition and encoding effects in the event-related brain potential. *Psychophysiology*, 33, 491-506.
- Wagner, A. D. (1999). Working memory contributions to human learning and remembering. *Neuron*, 22, 19-22.
- Wagner, A. D., Schacter, D. L., Rotte, M., Koutstaal, W., Maril, A., Dale, A. M., Rosen, B. R., & Buckner, R. L. (1998). Building memories: Remembering and forgetting of verbal experiences as predicted by brain activity. *Science*, 281, 1188-1191.
- Weyerts, H., Tendolkar, I., Smid, H. G. O. M., & Heinze, H.-J. (1997). ERPs to encoding and recognition in two different inter-item association tasks. *NeuroReport*, 8, 1583-1588.
- Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*, 46, 441-517.
- Yovel, G., & Paller, K. A. (2004). The neural basis of the *butcher-on-the-bus* phenomenon: when a face seems familiar but is not remembered. *Neuroimage*, 21, 789-800.

BIOGRAPHICAL SKETCH

Brian Howland was born in Washington, D.C., on June 13, 1961. He attended high school at James Madison High School in Vienna, Virginia, and graduated in 1979. He attended the College of Wooster in Wooster, Ohio, and graduated with a B.A. in economics in 1983. Upon graduation, he attended Washington and Lee University School of Law from which he graduated in 1986. He was engaged in the private practice of law in Virginia, and subsequently, Pennsylvania for almost five years. In 1993, he enrolled in graduate school in the Department of Psychology at the University of Florida, concentrating in cognitive psychology. He received the Master of Science degree in 1997 and will receive the Doctor of Philosophy degree in August 2005.