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An event-related potential investigation of the neural representations that support familiarity-based picture recognition

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**An event-related potential investigation of the neural
representations that support familiarity-based picture recognition**

by

Moses Michael Langley

A dissertation submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY

Major: Psychology

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Ames, Iowa

2010

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*To Ivan, ...for your constant support and encouragement.
I could not have done this without you.*

*To Anne, ...for your initial belief in me, and for your patience.
You continue to inspire me.*

*To Veronica, ...for being “mother hen.”
Your support was invaluable.*

Words cannot express how very grateful I am. Thank you.

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ABSTRACT

Most models of recognition memory assume that familiarity results from the matching of stimuli to the contents of memory. This matching process accumulates “evidence” that the stimulus was seen before, and when the evidence exceeds a criterion, a feeling of familiarity is experienced. Such models do not specify what constitutes “evidence,” and therefore offer limited insight into the specific attributes that make stimuli feel familiar. In two experiments, this dissertation examined the type of pictorial attributes that serve as “evidence” for familiarity-based picture recognition. Participants encoded briefly presented, masked pictures while event-related brain potentials (ERPs) were recorded. Of primary interest were ERPs for pictures that participants could not identify by name, as previous behavioral research suggests that such items are recognized on the basis of familiarity. Analysis of these encoding ERPs revealed that the global shape of subsequently recognized yet unidentified pictures was fully extracted during the picture’s brief presentation, but that their global object shapes were not successfully matched to object representations in memory (Exp 1 & 2). This result indicated that the memory trace for unidentified pictures contained limited conceptual information, and perceptual details that were abstract rather than detailed/episodic. ERPs recorded during retrieval revealed that the neural correlate of familiarity-based retrieval, the FN400, was present for unidentified pictures (Exp 1 & 2), and that the FN400 was more pronounced when participants were oriented toward processing perceptual, as opposed to conceptual, attributes of pictures during encoding (Exp 2). The behavioral measure of familiarity was consistent with this finding, which together implied that the largely perceptual representations in the pictorial memory trace were sufficient for later recognition of the unidentified picture, and that the pictures were more familiar when perceptual processing was greatest at encoding. The data presented in this dissertation indicate that familiarity-based picture recognition can be based on evidence that is largely perceptual and abstractly represented. The results are discussed within the context of perirhinal cortex models of familiarity, which suggest that picture familiarity is based on conjunctive features represented by the perirhinal cortex within the medial temporal lobe.

CHAPTER 1. INTRODUCTION

Humanity has a long-lived fascination with its ability to remember the past. This curiosity about human memory is evident upon considering that it has been a consistent topic of intellectual curiosity since the time of Aristotle. At its most basic, memory is the influence of prior experience on behavior and/or cognitive processes. This description is overly simplistic, however. Up close, human memory is a vast and flexible construct, involving many component processes that interact in complex ways. While the understanding of memory has advanced considerably since the days of Aristotle, even contemporary researchers struggle to unravel the layers of memory's elaborate architecture.

Some of the earliest *scientific* inquiries into human memory (i.e., Ebbinghaus, 1885; Nipher, 1876, 1878) focused primarily on identifying the parameters of conscious, everyday memory phenomena. Thus, it is unsurprising that the first published experimental study of human memory aimed to explain why, when writing a series of digits (e.g., serial number) from memory, the middle digits are more frequently forgotten than the digits at either end of the series (Nipher, 1876).

The curiosities of everyday memory phenomena continue to inspire the science of human memory; the *feeling of familiarity* is one such example. A feeling of familiarity is a vague impression of past experience with an event (or stimulus, e.g. person, place, object, tune; see Yonelinas, 2002). Albeit vague, this impression can still engender confidence that the prior event actually took place (e.g., Kim & Cabeza, 2007). What is curious about this phenomenon is that the sense of past experience may not be accompanied by the retrieval of any specific information about the prior event (i.e., recollection; Yonelinas, 2002). That is, with feelings of familiarity one may only have the

impression that “this was seen before,” without any specific mnemonic evidence to support that impression. Consequently, familiarity provides little means of determining whether or not the impression of past occurrence was based on an actually experienced event. For this reason, feelings of familiarity can be quite unsettling, especially when a decision must be based on a seemingly incomplete memory.

The feeling of familiarity is a common experience and has been referred to in written texts throughout history (e.g., Hume, 1777; Jewsbury, 1828; Lyon, 1996; Russell, 1921; Tucker, 1805). It is fairly safe to say that when one utters the phrase, “this feels familiar,” it is widely understood what is meant. Unfortunately, the origins (neuropsychological bases) of feelings of familiarity are not so well understood (for reviews, see Rugg & Curran, 2007; Rugg & Yonelinas, 2003).

The frequency with which people experience feelings of familiarity, together with a limited understanding of its bases, has made the nature of familiarity an active area of research amongst cognitive psychologists and cognitive neuropsychologists. There is substantial agreement that the strength of a feeling of familiarity is related to how well a given stimulus matches the contents of memory (e.g., Clark & Gronlund, 1996; ; Mandler, 2008; Rugg & Curran, 2007; Rugg & Yonelinas, 2003; Yonelinas, 1994, 2001; Wixted, 2007b). The degree to which the stimulus matches the contents of memory can also be conceptualized as the amount of “evidence” there is for the stimulus’ having been encountered previously. When sufficient “evidence” is present, one will accept that the stimulus was, in fact, encountered (for a detailed account of what qualifies as sufficient, see Bröder & Schütz, 2009).

There is general agreement that familiarity is cognitively impenetrable and, accordingly, the observer remains unaware of the type of “evidence” supporting the

feeling of familiarity (Lyon, 1996). The large majority of models of familiarity are silent about the precise types of information that constitute (or do not constitute) “evidence.” Hence, regardless of whether it is known that familiarity is based on an evaluation of the available evidence, so long as the nature of the evidence remains unspecified, it will be difficult for researchers to answer the fundamental question of, “*what makes something seem familiar?*”

Approach

This dissertation describes the use behavioral and noninvasive neuromonitoring measures to investigate the nature of the “evidence” supporting familiarity-based memory for pictures. As explained above, understanding the nature of the “evidence” supporting familiarity-based memory is essential for understanding why some previously encountered stimuli feel familiar while other previously encountered stimuli do not. It is also important for theory, as identifying the types of evidence that can support familiarity may allow for the reconciliation of various classes of recognition memory models. Establishing types of evidence could also have more practical implications. For example, familiarity-based recognition tends to be relatively inaccurate (Reder, Nhouyvanisvong, Schunn, Ayers, Angstadt, & Hiraki, 2000). Identifying the strongest types of evidence may prove useful in developing strategies for reducing the inaccuracy of familiarity-based memory, which would be especially relevant for segments of the population thought to rely more on familiarity to recognize stimuli in the environment (e.g., older adults, amnesics).

The general approach of the present study is to narrow the range of information that can serve as evidence for later familiarity-based judgments. The logic is that restricting the range of potential evidence at encoding will facilitate the identification of

the type of evidence critical for successful familiarity-based recognition. To restrict the range of potential evidence, pictures at encoding were presented briefly and masked, making identification of the pictures difficult. During these brief presentations, it is assumed that only a subset of information inherent to a given picture will be encoded and stored in a memory trace. Whether or not a picture can be identified by name during a given encoding trial will serve as a marker for sufficient restriction. The range of potential evidence will be considered sufficiently restricted if the picture could not be identified.

For such an approach to be informative, picture presentation must be brief enough (and masking heavy enough) to prevent identification on approximately half of the encoding trials. Conversely, presentation must not be so brief that it prevents the extraction of any information that could aid subsequent memory. In other words, pictures must be presented in a way that many of them are unidentifiable during encoding but also recognizable at retrieval. Previous studies using a procedure such as this (Langley & Cleary, 2008; Langley, 2008) have established the appropriate timing to achieve balance and this timing has been adopted here (see Chapter 6 for details).

Event-related potentials (ERPs) were recorded both during encoding and retrieval. The ERPs recorded during encoding can provide vital information about the degree to which the unidentified pictures undergo specific stages of perceptual and conceptual processing. This information can then be used to make inferences about the type of stimulus attributes most likely to be present in the memory trace (i.e., potential evidence). Manipulations of participants' orientation to perceptual and conceptual information during encoding may be able to further specify the stimulus attributes that are stored in the memory trace (Stenberg, Johnansson, & Rosén, 2006). ERPs

recorded during retrieval can also provide crucial information about the processing involved in matching the test picture to the contents of memory. By manipulating both (a) participants' orientation toward perceptual or conceptual stimulus attributes during retrieval, and (b) the degree of perceptual matching between test picture and what was encoded, the nature of the evidence supporting familiarity may be further specified.

Organization

Chapter 2 describes the qualitative experience of familiarity, how various models have characterized familiarity, and how familiarity is commonly measured behaviorally. Chapter 3 introduces a noninvasive neuromonitoring measure (i.e., ERPs) that has proven useful for indexing (in real-time) the neural activity occurring as cognitive processes unfold. The advantages and disadvantages of using ERPs are also discussed. Chapter 4 reviews how the ERP measure has been used to study memory, what has been learned, and why its use is desirable for the present study. Chapter 5 focuses specifically on what ERPs have revealed about the sequence of neural activities associated with the processing of perceptual and conceptual attributes of objects and pictures. Here, it is shown how the literature concerning the neural correlates of object identification can speak to the perceptual and conceptual processes that occur during the encoding of pictures. This knowledge is then merged with what is known about the perceptual and conceptual processes that occur during memory retrieval of pictures. Chapter 6 introduces the motivation behind Experiment 1, its methods, results and discussion. Chapter 7 introduces the motivation behind Experiment 2, its methods, results, and discussion. Chapter 8 is the general discussion, in which the results from Experiments 1 and 2 are discussed within the context of perirhinal cortex models of familiarity-based recognition.

CHAPTER 2. FAMILIARITY

Passages from century-old literature show that it has long been understood what is meant when someone states that s/he is experiencing a *feeling of familiarity* (e.g., Baldwin, 1893; Calkins, 1901). In fact, it appears that the feeling of familiarity is largely unique and unmistakable. The following quote describes, almost humorously, the *experience* of familiarity:

“What again happens when we meet with a person who is strangely familiar to us. The ‘strange’ familiarity consists in the arousal of a number of specific representations, many of which are recognized as incongruous and are rejected. Representations rise and revolve round that percept. The mind tingles with cognitive anxiety, with mental throes on the eve of giving birth to the specific associations, resulting in final recognition. This peculiar condition of subexcitment of representative elements started by the perception of an object constitutes the state which is termed the sense of familiarity. *Familiarity is vague recognition*, recognition not as yet made specific” (Sidis & Goodhart, 1904, p. 46).

This description of the experience of familiarity is, more or less, in agreement with my own view (albeit not as dramatic as described above). As the quote suggests, experiencing something as familiar can at times seem like a cruel trick of the mind. A tortuously vague sense of recognition—a sensation strong enough to inspire some degree of confidence in prior occurrence, yet absent of the smallest recollection on which to justify this level of confidence. Despite the frequent frustration that this feeling causes, familiarity can actually be quite useful. In an extension of the above example, a sense of familiarity can inform the decisions one makes after encountering a person that one cannot identify or cannot “recollect” meeting. During such an encounter, as the familiar individual initiates a conversation, does one:

- a) Proceed with a smile, pretend to remember this person, and continue the desperate search of your memory? Or
- b) Wait for the appropriate moment and politely ask, “Umm... Have we met?” or, “I’m sorry, but what was your name again?”

If there is a strong sense of familiarity for this individual, it may pay off to feign remembering until something that the familiar person says triggers recollection. If one has in fact met the individual, this tactic (informed by your sense of familiarity) may prevent embarrassment and spare the acquaintance from feeling unmemorable. Alternatively, if there is no inkling of familiarity for this person whatsoever, you might be more prone to accept the embarrassment of having to ask, “Have we met?” After all, maybe this person has mistaken you for someone else and your lack of familiarity reflects the fact that the two of you have never met. In either case, an assessment of familiarity (or lack thereof) is useful because it can guide your decisions in situations in which no other information is immediately available.

On the Nature of Familiarity: Descriptive, Statistical, and Neuroanatomical Models

What follows is a review of descriptive models of recognition memory. The purpose of this review is to provide perspective on the various ways in which the nature of familiarity has been described. The experiments reported here are primarily concerned with recognition that is familiarity-based, and so this review does not describe hypotheses related to recollection specifically. The breadth of this review is wide but selective, emphasizing theories proven most influential over the past three decades.

Signal Detection Models. Discriminating between previously experienced

events and novel events involves memory processes and a decision process. One difficulty in modeling memory is determining how to distinguish between the memory and the decision processes. The initial appeal of signal detection models was that they accounted for both the decision and the memory processes.

As applied in memory research, signal detection theory (see Macmillan & Creelman, 2005; Parks, 1966) assumes a response to most environmental stimuli that an observer encounters. Such stimulus responses are characterized as “signals”. The more experience that is gained with stimulus, the stronger the signal (or response) to it will be. Thus, if an observer were to study a list of stimuli, and were later presented with a second series of stimuli (some old, some new), the observer should be able to discriminate the old stimuli from the new stimuli on the basis of their “signal strength.” For each stimulus, signal strength is compared to a criterion set by the individual. When the signal satisfies the criterion an “old” response may be given, indicating that one recognizes the stimulus as studied. Such a signal could be the amount or degree of familiarity a participant experiences when presented with a stimulus, for example. Of course, some stimuli are inherently more familiar than others (regardless of their study status). Therefore, a variable that represents the strength of a specific test-stimulus must vary over a range of values. The distributions of the strength variable are separate for old stimuli and new stimuli, and the distance between the old and new distributions increases as the signal strengths of old stimuli increase. Thus, the distance between the distributions can be used to quantify the degree to which one is discriminating old stimuli from new stimuli (also referred to as “memory strength”).

The Atkinson and Mandler Models. In Atkinson and colleagues’ (Atkinson & Juola, 1974; Atkinson, Hertmann, & Wescourt, 1974) model, familiarity reflects the

activation of nodes in a lexical network, with each node in the network representing a previously encountered word/object. When one encounters a word/object, the stimulus's node becomes temporarily more active than the other nodes, with this heightened activation decreasing slowly over time. It is the assessment of the relative levels of activation that allows one to discriminate old from new stimuli based on familiarity. Atkinson described the activation of old versus new stimuli as resulting from perceptual, as opposed to conceptual, stimulus attributes. In this model, familiarity processes precede recollection, with recollection occurring only when familiarity is insufficient recognition to occur.

Mandler's (e.g., 1979, 1980) view of familiarity is very similar to that of Atkinson and colleagues, in that familiarity increases following exposure to stimuli. Like in the Atkinson model, Mandler also posited that familiarity is faster acting than recollection. However, he departed from Atkinson with familiarity being independent of, and operating in parallel with, recollection. Another difference is that the increased 'activation' results specifically from the successful integration of a stimulus's perceptual features in memory, the products of which can support both explicit and implicit memory processes¹.

According to Mandler (1980, p. 255), "...the phenomenal experience of familiarity can be best assigned to a process of intrastimulus integration. Repeated exposure of an event focuses organizational processes on the perceptual featural, and intrastructural

¹ An example of *implicit memory* can be seen during instances in which past experience improves performance on a task, or facilitates a cognitive process, without one being consciously aware that the past experience is being influential. An example of *explicit memory* can be seen during instances in which a past experience improves performance on a task because one consciously and deliberately references memory for the experience with the intention of retrieving information relevant to the task. In short, implicit memory operates outside of one's intention and awareness, while explicit memory in most often used intentionally and the end result is always experienced

aspects of the event; intrastimulus organization involves sensory and perceptual integrations of the elements of the target event.” In other words, the integration process underlying familiarity concerns the relationship between the perceptual components of a visual stimulus. The more exposure one has with a particular stimulus, the more established the relationships among components become. When a stimulus is encountered, it is matched against representations in memory. If the representation of the component relations is well established, then there will likely be a greater match with the stimulus, which in turn yields strong stimulus familiarity.

Mandler (1979, 2008) further argued that if such ‘*perceptual familiarity*’ is insufficient to support recognition, then additional retrieval processes are engaged which seek, among other things, information pertaining to the target stimulus’s identity. Together, familiarity and identification account for the whole of recognition in Mandler’s model. With respect to recollection, Mandler described an underlying process of experienced-based “*elaboration*” that works to associate a stimulus’s representation with other representations in memory. This associative elaboration operates within a semantic (and presumably episodic) network. As experience with a stimulus grows, the strength and number of semantic associations between its representation and those of existing representations will increase (i.e., elaboration). The network within which these processes operate is searchable during retrieval attempts. Thus, relative to a poorly elaborated stimuli, well elaborated stimuli will have more numerous and stronger connections within the network, thereby increasing the likelihood that the stimulus will be retrieved. Mandler’s model also predicts that increasing amounts of time spent attempting to match perceptual stimulus features to feature patterns in memory leads to

consciously. These terms were first introduced by Graf and Schacter (1985).

a higher probability that elaborative retrieval processes will be engaged.

Fluency. Jacoby and colleagues (e.g., Jacoby, 1983; Jacoby & Dallas, 1981; Kelley & Jacoby, 1989) have argued that when recognition is not based on recollection it is based on the attribution of “processing fluency” (their take on familiarity). Fluency refers to the ease with which one perceives and processes stimuli. According to many familiarity-as-fluency hypotheses, previously encountered stimuli are more easily/fluently processed upon a subsequent encounter, merely due to the fact that they were processed before (this is also known as *priming*). One might attribute the enhanced, or more fluent, processing to prior experience with the stimulus, and thus be more prone to experience a sense of familiarity or remembrance. According to the early Jacoby model, such attributions may be based on the fluency elicited by either conceptual or perceptual priming (Kelley & Jacoby, 1989). Like the Mandler model, familiarity/fluency in the Jacoby model is independent of and operates in parallel with recollection.

The idea that attributions of any kind, fluency (Jacoby & Whitehouse, 1989), discrepancy (Whittlesea & Williams, 2000, 2001), or otherwise, can serve as the sole basis of explicit familiarity is a bitterly contentious idea. With regard to fluency attributions, a number of recent studies have provided convincing evidence that fluency does contribute to recognition memory. However, the degree to which it contributes depends on factors such as stimulus format or modality congruency between study and test (Miller, Lloyd, & Westerman, 2008; Westerman, Miller, & Lloyd, 2003), the expectation that test stimuli will be fluently processed (Westerman, Lloyd, & Miller, 2002), and the degree to which fluency seems relevant or diagnostic for recognition decisions (Lloyd, Westerman, & Miller, 2003; Miller et al., 2008; Westerman et al., 2002, 2003). While the ephemeral nature of fluency’s contribution to recognition makes it an

unlikely explanation for familiarity-based recognition, the fact that it does contribute in an intricate way (Westerman, 2008) should not be ignored.

Global Matching Models. The term 'global matching' describes a class of models whose primary assumption is that recognition is based solely on familiarity (Clark & Gronlund, 1996). The global matching process combines all of the information present at the time of the retrieval attempt into a single, conglomerate memory probe (CMP). This CMP accesses a broad swatch of memory, and activates matching memory trace information (Clark & Gronlund, 1996). The degree to which the CMP activates stored information is a function of how well the CMP and stored information match, or share similar attributes. There are many global matching models, the majority of which are variants of the signal detection model (Clark & Gronlund, 1996). Some of the more influential global matching models include the TODAM model (Murdock, 1982), the SAM model (e.g., Gillund & Shiffrin, 1984), and MINERVA 2 (Hintzman, 1988). These models share the same basic principles, but the specifics of these models vary considerably. For reviews of global matching models, see Humphreys et al. (1989) and Clark and Gronlund (1996).

Moscovitch's Model. In Moscovitch's (1995a, 1995b, 2000) theory of explicit memory, he proposes that it begins with the "conscious apprehension of a stimulus event" (Moscovitch, 2000, p. 612) and proceeds to describe his theory at the level of the brain. Assuming successful 'apprehension' takes place, Moscovitch argued that neurons in the neocortex that support conscious experience become part of the memory trace (due to binding mechanisms in the medial temporal lobe). Thus, the memory trace for an event consists of a network of neurons in both the medial temporal structures and the neocortex, with medial temporal regions facilitating the search of information stored

in the neocortex. When network reactivation occurs, both the stimulus feature representations *and* the neural elements that gave rise to the original conscious experience become active. This explains why recollecting information is like 'mental time travel,' because recovering episodic information for a previous event also entails recovering the conscious awareness one experienced as the event unfolded.

It is possible, however, to lose both the information regarding stimulus features and the information regarding the conscious experience at various points throughout the distributed neural network. Loss of information can occur either from improper consolidation or during retrieval. Retrieval of a relatively intact memory trace that includes contextual and stimulus feature details would likely yield recollection. However, the retrieval of an impoverished memory trace that is lacking in spatio-temporal context and stimulus feature details, while still containing information related to the conscious experience, would likely yield only familiarity. If the trace did not retain information regarding the conscious experience of the event, only implicit memory would be possible. As such, Moscovitch (1992, 1993, 2000) argued for the idea that familiarity is functionally and anatomically distinct from priming (and semantic memory), and is instead dependent upon mechanisms that support explicit memory (not further specified). Lastly, it is important to note that Moscovitch's (e.g., 2000) theory is agnostic as to whether recollection and familiarity are fundamentally different neural processes. However, his proposal does allow for the *subjective experience* of both recollection and familiarity to emerge from a single memorial process and, therefore, side-steps the single-process dual-process debate.

Behavioral Measures of Familiarity

Cognitive psychology is rich with methodologies for measuring the various facets

of the human mind. When it comes to recognition memory measures, there are many measures and each has its own merits. Moreover, several of the more prominent memory measures have influenced theory over the years. To provide perspective, several of the most prominent measures are described here. Signal detection analysis receives the most thorough treatment because this is the measures has been adopted for the experiments of this dissertation.

Signal Detection Analysis. In a yes-no (YN) memory task (e.g., Murdock, 1965), the presentation of a test-stimulus that was actually studied is termed a “signal trial,” and participants are to respond “yes” during such trials. The presentation of a test-stimulus that was not studied is termed a “noise trial,” and participants are to respond “no” during these trials. When a participant responds “yes” on a signal trial, it is referred to as a hit. The proportion of correctly recognized stimuli is called the hit rate and this equals the proportion of the signal distribution that has satisfied the decision criterion set by the participant. Similarly, when a participant endorses an unstudied test-stimulus as old, it is called a false alarm, and the proportion of false alarms made, the false alarm rate, equals the proportion of the noise distribution that has satisfied the participant-set decision criterion (Bernbach, 1971).

The hit and false alarm rates reflect two factors, response bias and the extent to which the signal and noise distributions overlap (i.e., sensitivity). The usefulness of signal detection theory stems from its ability to separate the two. Sensitivity, or d' , is derived from the hit and false alarm rates and is a measure of the distance between the signal and the noise distributions. A d' value of zero indicates no discrimination between old and new test-stimuli, while values reliably greater than zero imply, overall, successful discrimination between old and new stimuli (Macmillan & Creelman, 2005).

According to equal-variance signal detection, response bias does not affect sensitivity if two assumptions are met: (1) The signal distribution and the noise distribution are normal, and (2) the signal distribution and the noise distribution have the same standard deviation (or have equal variances). If either assumption is violated, sensitivity will vary with response bias and the two cannot be separated. As it turns out, these assumptions are suspect with respect to performance on yes/no tasks and the equal-variance model is not recommended for recognition memory data (Wixted, 2007a,b).

The preferred signal detection model is the unequal-variance model (Wixted, 2007a,b), which allows the distribution of the old stimuli to differ from the distribution of the new stimuli. Preference for the unequal-variance model is justified on the grounds of substantial empirical evidence and common sense. First, meta-analyses (Glanzer et al., 1999; Ratcliff et al., 1992) on approximately 30 years of recognition memory receiver operating characteristic (ROC) data have shown that the variance of the old stimulus distribution is significantly greater than 1.0, generally observed to be around 1.25. This long and consistent history implies that the equal-variance model (which assumes an old stimulus variance distribution equal to 1.0) is unlikely to be correct. Second, and as Wixted (2007a, p. 154) points out, it is instructive to think of old stimuli as new stimuli that have undergone a boost in memory strength as a function of being encoded during their presentation in the study-list. If each stimulus in the study-list received an equal boost in memory strength after being encoding, then the variance of the old stimulus distribution should remain the same. In other words, if the variance of the soon-to-be old stimulus distribution equaled 1.0 prior to encoding and *during* encoding each stimulus received an equivalent boost in memory strength, then the variance of the

distribution should not change and the unequal-variance model would hold. However, such an occurrence is unlikely, to say the least.

The boost in memory strength that each stimulus receives during encoding *will* vary across stimuli, as each stimulus possesses a somewhat unique “individuality,” differing along variables such as salience or ‘*fluency*.’ Moreover, other factors that are potentially unrelated to the stimuli will no doubt differ across the encoding episode—attention, for example. Thus, encoded stimuli receive not only a boost in memory strength but also a boost in variability, thereby rendering an equal-variance account implausible. In using the unequal-variance model, an appropriate estimate for the variance of the old stimulus distribution (σ_{old}) can be determined by calculating the slope (s) of the z-ROC and using the following equation: $\sigma_{old} = 1/s$ (Macmillan & Creelman, 2005).

It is important to note that signal detection theory’s description of recognition along a single, unidimensional strength axis does *not* imply that recognition memory itself operates by a single process (Kelley & Wixted, 2001; Wixted, 2007b). On the contrary, the memory strength variable can represent the joint contributions of recollection and familiarity. The key assumption here is that recognition memory is most often a mixture of the two recognition processes rather than one or the other (Wixted, 2007b).

As a measure of old/new discrimination, one weakness of signal detection theory is that there is no way to estimate the contributions of recollection and familiarity to overall recognition. Most methods whose measures attempt to calculate estimates of the two processes have encountered considerable obstacles (as described below). A second issue, with respect to the unequal-variance model, is that the model has

difficulty accounting for data that are indeed characterized by a slope equal to 1 and equal distributions. If merely being encountered in a study-list adds variance to the old item distribution, regardless of how poor later memory is, how can it explain statistically reliable indices of discrimination that are also characterized by old and new distributions of equal variance?

Remember-Know. Unlike the signal detection theory analysis, the remember-know procedure is unambiguous in its assumption that the experience of recognition memory involves two processes. The remember-know procedure was devised by Tulving (1985) as a means of differentiating between the subjective experiences of recollection and familiarity, and its use within the recognition memory literature has been prolific since the publication of seminal works in the late 1980's and early 1990's (e.g., Gardiner, 1988; Gardiner & Parkin, 1990; Yonelinas & Jacoby, 1995). The original premise of this procedure was simple: Merely ask subjects to introspect on their subjective memorial experience. For each test item presented, subjects are asked if they recognize a given test item because they "remember" encountering it during the encoding phase, or whether they recognize the test item because they simply "know" it was presented. Participants in studies using this procedure are cautioned to provide a remember response only if they can recollect the test item, and respond know if the item only seems familiar (if participants do not recollect the item, they respond "new").

As originally proposed, the remember-know procedure assumed that recollection and familiarity were dependant processes (Gardiner & Parkin, 1990). Estimates of recollection and familiarity under this assumption are simply the proportion of studied items given a remember response, and the proportion of studied items given a know response, respectively. The currently accepted assumption is that recollection and

familiarity are independent processes (Yonelinas, 2001; Yonelinas & Parks, 2007; but see Malmberg, 2002, and Wixted, 2007a,b). The means of deriving estimates of recollection and familiarity under the independence assumption (Yonelinas & Jacoby, 1995) is to calculate the proportion of remember responses (R) for estimates of recollection and to calculate the proportion of know responses divided by the proportion of responses that were not “remembered” ($F = K/(1 - R)$).

Advantages of this procedure are that estimates of recollection and familiarity are easily derived, and that the instructions to participants are simple and intuitive. However, an inescapable liability of the procedure is that the measures of recollection and familiarity are based on participants’ subjective, qualitative assessments of their memories. *Experimental* psychology was, in part, adopted by researchers to end the practice of collecting non-objective, unverifiable introspection as data on which to make inferences about cognition (Overgaard, 2006).

Another possible liability is that “know” judgments may always, or on some occasions, reflect recognition supported by recollection (rather than recognition in the absence of recollection). Supporting this possibility is a study by Wais, Mickes, and Wixted (2008) showing above chance source memory (which involves recollection) across trials on which participants responded “know.”² Wais et al. argued that remember and know judgments actually reflect varying degrees of recollection. This result is problematic for theories of recognition that assume the contribution of two

² The term *source memory* refers to memory for the specific contextual details related to the previous occurrence of a stimulus or event. As an example, assume that one is presented with words, some spoke in a male voice and others spoken in a female voice. Three hours later one is given a memory test for the spoken words. On the test, one is asked whether a particular word was heard previously, and, if so, what gender the voice was for that specific word. One’s memory for the gender of the voice would be considered source memory. Evans and Thorn (1966) were some of the first researchers to examine memory for source, but the term “source memory” was not regularly use until

independent processes (recollection and familiarity). As mentioned, much of the empirical support for the dual-process view comes from the results of remember-know studies. If Wais et al.'s claims to be believed, it would require a single-process interpretation of the remember-know literature, thereby reducing much of the current behavior data supporting the dual-process view.

Process-Dissociation. Jacoby (1991) devised the process-dissociation procedure to obtain quantitative estimates of the recollection-based and familiarity-based components of explicit recognition. In the original version of the procedure, participants initially viewed a list of words under incidental encoding instructions. Later, participants heard a second list of words under intentional encoding instructions. Following the presentation of both lists, participants engaged in a recognition memory test consisting of an equal number of words from each list and new words. In one testing condition, participants were to endorse a word as studied, so long as it had appeared in one of the two word lists (inclusion condition). In a second testing condition, participants were to endorse a word as studied only if it had appeared in the intentionally encoded word list (exclusion condition); words that appeared in the incidentally encoded list were to be rejected as unstudied. Jacoby derived the estimates of recollection and familiarity in accordance with the following logic:

Assuming that recollection and familiarity are independent processes, the probability of endorsing an incidentally encoded word as studied under inclusion instructions should equal the probability of only recollecting (R) an incidentally encoded word plus the probability of the words only being familiar (F), minus the probability that the incidentally encoded word is both recollectable *and* familiar, $P(\text{Old}) = (R + F) - (RF)$.

approximately two decades later (e.g., Shimamura & Squire, 1987).

This essentially amounts to saying that one can recognize an incidentally encoded word in the inclusion condition if one recollects it or if one deems the word familiar.

For incidentally encoded words in the exclusion condition, the probability of endorsing a word as old should equal the probability that the word is familiar minus the probability that the word is both recollectable and familiar $P(\text{Old}) = F - RF$. Remember that in the exclusion condition, participants are to reject all incidentally encoded words as unstudied. Therefore, participants should only endorse these words as studied if the words are sufficiently familiar (as a result of having been presented recently), but not recollectable. Jacoby (1991) subsequently calculated the contribution of recollection to memory performance by subtracting exclusion from inclusion, $R = ((R+F)-(RF)) - (F-(RF))$. After solving for R, F can be derived, $F = (F-(RF))/(1-R)$.

The liability of this procedure is that the equations for estimating familiarity and recollection in this procedure are fundamentally flawed because the equation induces item selection effects (Russo, Cullis, & Parkin, 1998). The flaw in the equation is most considerable in the estimates of familiarity. The equations lead to familiarity estimates being based on exclusively nonrecollectable items, and the bias that this induces will increase under conditions in which items are particularly recollectable. Levels of processing manipulations would achieve significant biasing in the process estimates. Indeed, Russo et al. observed this very pattern when introducing a levels of processing (size congruency) manipulation. They also observed that the shallower the encoding was at study, the greater the estimates of familiarity became. Such outcomes violate the procedure's key assumption of the processes being independent.

On the Role Perceptual vs. Conceptual Processing in Dual-Process Recognition

Early research on the dual-process approach to recognition memory suggested

that conceptually driven processes supported an effortful, elaborative recollection-based memory, whereas implicit-like perceptually-based processes supported automatic familiarity-based memory (e.g., Jacoby & Dallas, 1981; Mandler, 1979, 1980; Tulving, 1985; Whittlesea, 1993). Departure from this view has come about for three reasons: First, subsequent studies (e.g., Wagner, Gabrieli, & Verfaellie, 1997) have shown clear dissociations between the familiarity associated with explicit recognition and familiarity associated with implicit manifestations of memory. Second, several studies imply a substantial role of perceptual and conceptual processing in explicit familiarity-based recognition (e.g., Ally & Budson, 2007; Boldini, Algarabel, Ibañez, & Bajo, 2008; Boldini, Russo, Punia, & Avons, 2007; Ecker & Zimmer, 2009; Ecker, Zimmer, & Groh-Bordin, 2007; Groh-Bordin, Zimmer, & Ecker, 2006; Grove & Wilding, in press; Schloerscheidt & Rugg, 2004; Stenberg et al., 2006; Wagner & Gabrieli, 1998). Third, a line of research demonstrates quite well that recollection is fairly sensitive to changes in the perceptual characteristics of pictorial stimuli between study and test (e.g., Ally & Budson, 2007; Gardiner, Gregg, Marshru & Thaman, 2001; Gardiner, Konstantinou, Karayianni & Gregg, 2005; Rajaram, 1996; Verfaellie, Cook & Keane, 2003; Yonelinas & Jacoby, 1995). More specifically, research demonstrating the role of recollection in picture memory has centered on what are known as perceptual matching effects. A perceptual match occurs when a stimulus is in no way altered in terms of its sensory features between study and test. For example, a robust finding in research on recognition memory is that when there is not a perceptual match between a stimulus's study and test presentations, recognition memory performance declines. As a testament to its pervasiveness, perceptual matching effects in recognition memory have been shown to occur for both verbal stimuli (e.g., Reder, Dinavos, & Erickson, 2002) and pictorial

stimuli (e.g., Snodgrass, Hirshman, & Fan, 1996). However, in some regards the research on perceptual matching effects has brought about more questions than it has answered.

This dissertation is concerned with the contributions of perceptual and conceptual processing to familiarity-based recognition, and studies of perceptual matching effects in recognition have been somewhat informative on this matter. Of the perceptual matching effects that occur within modality (e.g., visual) and within a single visual form (e.g. pictures alone as opposed to pictures being changed to words), the most widely examined matching effect in recognition memory is probably the size congruency effect (which is a benefit to recognition memory when study and test pictures are the same size (see Jolicoeur, 1987). In what follows, I describe some of the research on the size congruency effect to illustrate the point that to-date the relative contributions of perceptual and conceptual processes to both recollection and familiarity are far from well defined.

Among researchers who have examined pictorial size congruency effects from a dual-process perspective, most have searched for differential effects of size congruency on remember and know judgments. In these studies, declines in the accuracy of recognition, as seen in remember responses, would imply a sensitivity of recollection to perceptual information. Declines in the accuracy of recognition, as seen in know responses, would imply a sensitivity of familiarity to perceptual information. Many studies have shown size congruency effects in remember judgments (Gardiner, Gregg, Marshru & Thaman, 2001; Gardiner, Konstantinou, Karayianni & Gregg, 2005; Rajaram, 1996; Verfaellie, Cook & Keane, 2003; Yonelinas & Jacoby, 1995). If one accepts the idea that remember responses primarily reflect the contribution of recollection and know

responses primarily reflect the contribution of familiarity (for compelling data against this idea, see Wais et al., 2008), it would appear that such studies support the idea that recollection is sensitive to perceptual manipulations. The question that remains is whether familiarity is also sensitive to size congruency and perceptual matching effects.

Indeed, some evidence does suggest that familiarity-based picture recognition may also show size congruency effects. In their Experiment 2, Yonelinas and Jacoby (1995) initially found size congruency effects reflected only in *remember* responses. They argued that this observation was an artifact resulting from a theoretical assumption of the Remember/Know procedure, namely that the memorial processes underlying *remember* and *know* responses (recollection and familiarity, respectively) are dependent. However, when the assumption of independence between *remember* and *know* responses was adopted, wherein the proportion of *know* responses were divided *only* by the proportion of the responses that are not *remember* responses, a size congruency effect was observed in *remember* and *know* responses. This finding was in agreement with the results of Yonelinas and Jacoby's Experiment 1 (a process-dissociation experiment) that was also suggestive of a familiarity-based size congruency effect.

For reasons not initially obvious, however, other studies of size congruency (e.g., Verfaellie et al., 2003) that have used Yonelinas and Jacoby's (1995) independence Remember/Know procedure have failed to find a size congruency effect for *know* responses (but see p. 110 of Verfaellie et al. for speculation as to why). Specifically, Verfaellie et al. failed to find size congruency effects in amnesic patients. Many studies have shown that certain types of amnesia are characterized by impairments of recollection primarily (e.g., Aggleton & Brown, 1999). Thus, if amnesic patients' explicit

recognition operates primarily on familiarity processes, then the fact that the amnesic patients failed to show any manifestation of size congruency effects suggests that size congruency is in fact a recollection-based effect. Such inconsistencies in the literature cast doubt on the idea that familiarity is capable of supporting size congruency effects and matching effects in general.

Complicating the picture even further is a study by Gardiner et al. (2001) wherein size congruency effects were only in *remember* responses under some conditions and in *know* responses under other conditions. In the first of two experiments, Gardiner et al. had participants study a series of line drawings under divided or full attention conditions. During test, participants made old/new judgments for each test stimulus. For those stimuli given old judgments, participants were asked to indicate, subjectively, the source of their memory (i.e., recollection or familiarity) using *remember* or *know* responses, respectively. Interestingly, Gardiner et al. reported that full attention at encoding produced size congruency effects that were reflected in *remember* responses only, a finding that replicates Rajaram (1996). In contrast, divided attention at encoding (or impoverished encoding condition) produced size congruency effects that were reflected in only *know* responses.

So, like Yonelinas and Jacoby (1995), Gardiner et al. found evidence suggesting that familiarity can support size congruency effects. However, unlike Yonelinas and Jacoby, Gardiner et al. did not observe that recollection-based and familiarity-based congruency effects occur under the same conditions. Gardiner et al. had posited that impoverished encoding conditions would lead to recognition based largely on familiarity and less on recollection. This idea stemmed from prior work (Gregg & Gardiner, 1994; also see Gardiner & Gregg, 1997) suggesting that when rapidly presented stimuli are

used to create impoverished encoding conditions, subsequent recognition is based primarily on stimulus familiarity. The idea that impoverished study conditions might lead to recognition based primarily on familiarity is an idea that, if true, might have significant implications for the study of familiarity in the absence of recollection.

The size congruency studies just described all used the remember-know procedure to separate recollection from familiarity, yet there is little agreement among their results. One explanation for this may be that “remember” and “know” judgments do not actually reflect recollection and familiarity, but rather varying degrees of recollection. If true, the contribution of recollection to “know” judgments could explain why in some conditions size congruency effects are observed in both remember and know judgments (e.g., Yonelinas & Jacoby, 1995) or remember judgments alone (Gardiner et al., 2005) in other conditions.

Nevertheless, it seems clear that perceptual matching manipulations (such size congruency) can be used to influence the role of perceptual and conceptual processing in recognition memory. It has also been shown that demands of the memory task may influence the degree to which perceptual and conceptual information contributes to recognition. For example, Stenberg et al. (2006) have shown that factors such as retrieval instructions can influence the degree to which participants rely on perceptual and conceptual information. With an inclusion/exclusion manipulation, Stenberg et al. showed that participants tended to rely more on perceptual information under exclusion instructions and more on conceptual information under inclusion instructions. It seems plausible that task demands could also affect the degree to which participants rely on perceptual and conceptual information. Might task demand be partially responsible for the discrepancies found between the aforementioned size congruency studies?

As mentioned, Gardiner et al. (2001) also reported size congruency effects exclusively in know judgments when participants were subjected to divided attention at encoding, whereas size congruency effects were found exclusively for remember responses under full attention conditions at encoding. If dividing participants' attention during encoding makes perceptual information less useful, accessible, or reliable during familiarity-based retrieval, then participants may rely more on conceptual information, leading one to predict greater effects of perceptual mismatching. This seems plausible given the rich conceptual/semantic processing that pictures receive relative to words (Paivio & Csapo, 1973). This idea is also consistent with Mandler's (1980, 2008) description of the integration process that underlies familiarity. Mandler argued that the strength of familiarity increases as a function of the degree of stimulus integration, which itself increases with the quality of encoding (e.g., repetition). If encoding is impoverished, then stimulus integration should be fairly weak. As a consequence, the degree of perceptual match between encoding and retrieval stimulus instantiations would be poor, which may lead to a reliance on conceptual processing. Unfortunately, Mandler's model is in fact silent on how conceptually/semantically based familiarity might operate.

Chapter 2 Summary

Within the last 35 years of behavioral research, the familiarity process has been described as (a) an increase in activation of a preexisting representation (e.g., Atkinson & Juola, 1973), (b) an increase in activation of a perceptual representation constructed through a process of in-traitem integration (e.g., Mandler, 1980), (c) perceptual or (d) conceptual fluency (Jacoby & Dallas, 1981), (e) an increase in activation of any representations across the entire memory network that match the stimulus (e.g.,

Hintzman, 1988), (f) signal strength (e.g., Macmillan & Creelman, 2005) or strength of a particular memory trace (e.g., Yonelinas, 2001), and (g) the reactivation of neocortical neurons representing only the conscious experience of a prior event (e.g., Moscovitch, 2000). Researchers generally agreed that familiarity is a fast-acting process, and there is more or less agreement that familiarity can be characterized as an increase of activation of some type of stored information. Familiarity may also solely support recognition (Hintzman, 1988), or it may operate in parallel with and independently of recollection (e.g., Yonelinas, 2001). Familiarity may be an attribution of priming (Kelley & Jacoby, 1989), or it may be functionally and anatomically distinguishable from priming *and* semantic memory.

Clearly, the characterization of familiarity and the neural network that supports it is not yet complete. Moreover, there is some cause for concern regarding the methods of estimating the contributions of recollection and familiarity to overall recognition memory performance. Lack of consensus on how to characterize familiarity and problematic process estimation procedures make interpreting the behavioral literature difficult. Questions regarding the role of perceptual and conceptual information in familiarity also remain to be addressed. The experiments presented here use an alternative procedure for assessing familiarity-based recognition, while also collecting physiological data that may aid in corroborating the behavioral results obtained. Chapter 3 describes the method and procedure for collecting the ERP data, and also describes some considerations in interpreting these data.

CHAPTER 3. ELECTROPHYSIOLOGY

An active topic in human memory research concerns the identification of the neural mechanisms that govern many aspects of human behavior. Many technologies now exist for assessing the relationship of a given brain region or neural response with a particular memory phenomenon. Such methods range from those capable of imaging areas of the brain that are highly active during memory encoding or retrieval, like *functional magnetic resonance imaging* (fMRI), to those capable of temporarily modulating the neuronal activity in specific areas of the cortex, like *repetitive transcranial magnetic stimulation* (rTMS). The methodology of the experiments described in this dissertation involve ERP, recording the spatial distribution and temporal dynamics of participants' neural activity occurring as memory-related cognitive processes unfold. The following will explain in detail (a) electroencephalography and the ERP technique, (b) considerations for interpreting the resultant data, and (c) why the technique is desirable for the research undertaken in this dissertation.

The Electroencephalograph

An electroencephalograph is an instrument that uses small electrodes, placed on the scalp, to record the electrical activity of the brain (i.e., electroencephalogram (EEG) see Figure 1). The neural origin of said activity (that is recordable at the scalp) is the sum of postsynaptic potentials from a large population of neurons (thousands to millions). The postsynaptic potentials, themselves, originate from the binding of neurotransmitters to receptors on the membrane of postsynaptic neurons (Fabiani, Gratton, & Coles, 2000). Binding causes the neuron's ion channels to open/close, leading to changes in the electric potential on the postsynaptic cell surface (Luck, 2005). In turn, postsynaptic potentials generate minute electrical fields that vary in voltage

across time.

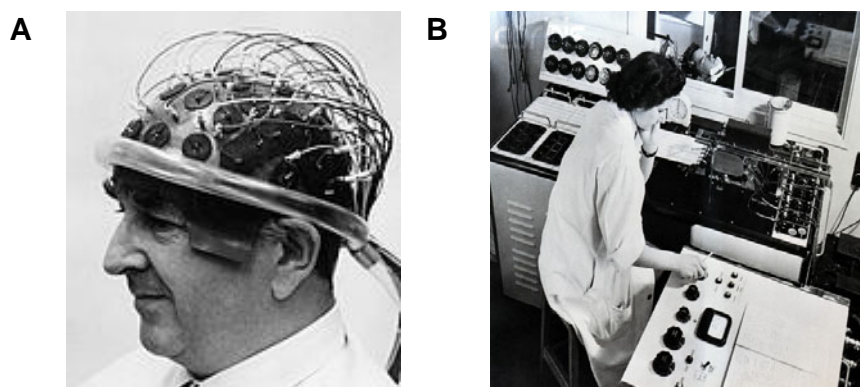


Figure 1. A vintage photograph of an early ERP system.

Because postsynaptic electrical fields are extremely weak by the time they reach the scalp (currents weaken as they spread), they must be amplified ($\times 10^3 - 10^6$) as they are recorded (Davidson, Jackson, & Larson, 2000). Postsynaptic potentials reach the scalp because the tissue between the scalp and the given neuronal population (neural generator) serves as a *volume conductor* (Fabiani et al., 2000). Not all neuronal activity reaches the scalp, however. For example, activity produced by a single neuron (or a small group of neurons) will not generally reach the scalp. Rather, the summed activity of a large neuronal population is usually sufficient in producing a level of activity detectable in the EEG. Criteria additional to the summation of neural activity are that individual neurons of a given population must (a) have synchronous activation and (b) be oriented such that their activity summates at the same region of the scalp (Fabiani et al., 2000). Therefore, only brain structures with particular spatial organizations can generate activity detectable at the scalp. But even brain structures with this type of organization are not guaranteed to elicit activity that can be detected at the scalp.

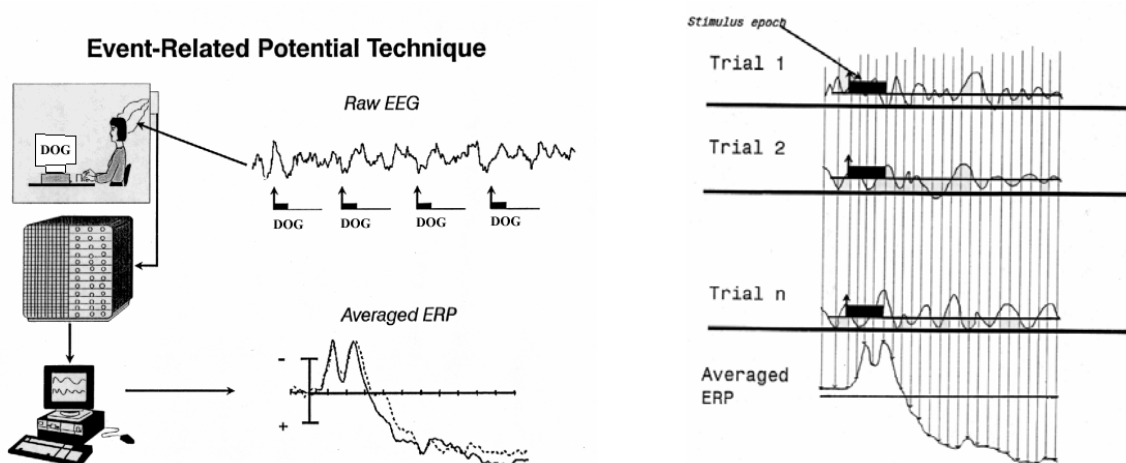


Figure 2. Event-Related Potential Technique.

The Event-Related Potential (ERP)

ERP is brain activity that occurs “in preparation for, or in response to, discrete events, be they internal or external to the subject” (Fabiani et al., 2000, p. 53). In other words, the ERP is a component of the larger EEG oscillation, but represents only that portion of the EEG that is elicited relative to a specified event in time. A common method of extracting ERPs from an EEG is to average sections of the EEG that maintain a constant temporal relationship with repeated occurrences of the specified event (see Figure 2). The logic for this method is as follows: EEG components *not* time-locked to the event of interest vary randomly across samples (assumed), and such random potentials will average out over samples leaving behind only the ERPs of each sample (Fabiani et al.). When examining the effects of experimental variables, 30-100 samples (trials) are generally recommended when averaging—although this number varies across discipline and is highly dependent upon the EEG signal in question, the number of other EEG signals present, the signal-to-noise ratio, and the degree to which artifacts are present in the data (Luck, 2005).

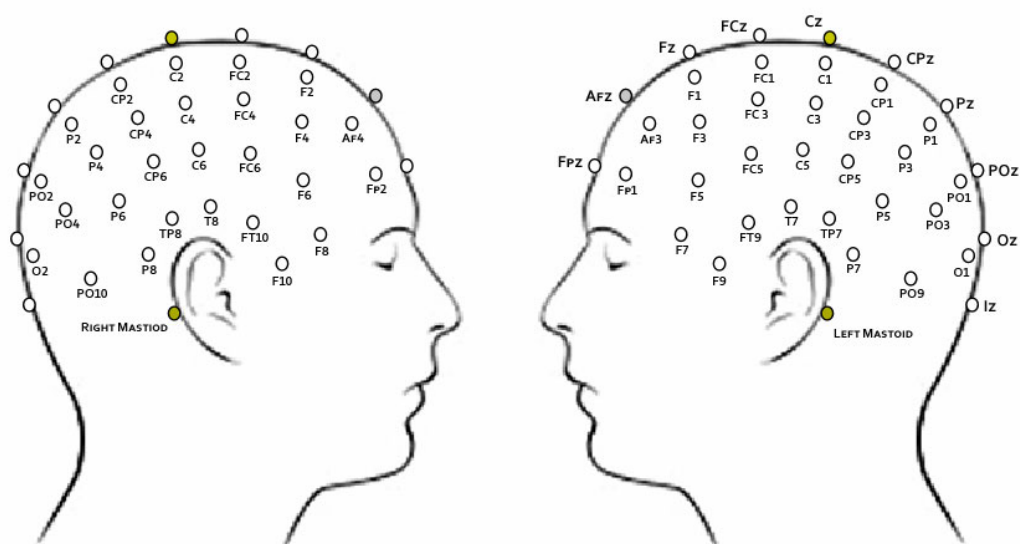


Figure 3. Approximate electrode location and distribution across scalp for the EEGs recorded in the experiments reported in this dissertation. Electrode Cz served as a reference during recording, and electrode Afz served as the ground electrode.

It is tempting to conceptualize an ERP waveform merely as the brain activity measured at a particular scalp site (See Figure 3). The EEG/ERP waveform actually reflects the *difference* between the voltage recorded at a specific electrode and the voltage at the *reference* electrode (the electrode(s) to which all other electrodes are compared). Conceptually, the reference electrode would index an electrically neutral location on the scalp. Unfortunately, no such electrically inactive site exists on the body. One method (of many) for circumventing this reference problem is to use a *common average reference* (used in this dissertation). Using a common average reference involves averaging the voltage across all electrodes as a reference to examine the activity at a given electrode (Davidson et al., 2000). The assumption here is that the

positive/negative variation in voltage across the head will average to zero (Davidson et al., 2000). This assumption is the most likely to hold when using moderate to high-density systems (> 32 electrodes) that maintain a reasonably even distribution of electrodes over the head (for other referencing methods, see Luck, 2005). The common average reference method is an accepted approach and appropriate under a variety of experimental conditions and only when moderate to high-density systems are used (Picton et al., 2000).

It is also tempting to conceptualize ERPs simply by the characteristics of their voltage deflections (peaks and troughs). However, the voltage deflections are most typically the expression of many summed *latent components*. The latent components are difficult to ascertain from a visual inspection of an ERP waveform because smaller latent components may have occurred simultaneously, summing at the same region of the scalp to contribute to the shape of the ERP. Thus, one important task involved in assessing an ERP waveform is approximating the number of components that may be contributing in a significant way to a particular ERP, which itself is a product of many averaged samples (Hillyard & Kutas, 1983).

Quantifying ERPs

Electrophysiologists have developed statistical techniques over the years that aid researchers in identifying latent components in ERP waveforms (Hillyard, 2009). The majority of these techniques are *correlation-sensitive*, meaning that they identify components based on the correlational structure of ERP data. More specifically, these techniques derive ERP components by grouping time points that vary in a correlated way (Luck, 2005).

Researchers can assess and interpret ERP and ERP component differences on

several distinct dimensions. For example, the *amplitude* of a particular component can imply the degree of neural activation and a component's functional response to a particular variable (Friedman & Johnson, 2000). The *latency* of a component implies the timing of neural activation, while the *scalp distribution* (or scalp topography) of ERP data implies an overall pattern of brain activity (Friedman & Johnson); ERP components are typically differentiated by their latency and scalp topography (Curran, Tepe, & Piatt, 2006). The specifics of how waveforms are differentiated, how components are identified, and how quantitative and qualitative differences are assessed statistically are described in Chapter 6.

When only ERP *magnitudes* differ between conditions, researchers generally consider the differences to be *quantitative*, and interpret them as reflecting a common neural generator at different levels of engagement (Allan, Robb, & Rugg, 2000). When ERPs differ only with respect to scalp distribution (or electrode location), researchers generally consider the differences to be *qualitative*, and interpret them as reflecting distinct neural generators, or different levels of engagement of the same generator (Allan et al., 2000). Whereas quantitative differences involve comparing conditions and effects at the same electrode(s), qualitative differences involve comparing conditions and effects across individual electrodes or groups of electrodes.

The Advantages/Disadvantages of ERPs

The practical advantages of ERPs are that the measurement of neural activity is a) noninvasive and b) inexpensive relative to other neuroimaging techniques. The *principal* advantage of ERPs, however, is the capacity to index the neural correlates of cognition in "real-time" (Wilding, 2001). Whereas with hemodynamic methods the temporal resolution can range between 3 and 5 seconds (e.g., fMRI) to ~30 and 60

sseconds (e.g., PET), with ERP the neural response can be measured on the order of milliseconds (Friedman & Johnson, 2000). This makes ERP particularly well suited for the study of human memory because most memory processes occur within the first second of stimulus processing. ERPs also provide researchers with a means of separating early memory processes with similar time courses, a task that has proven difficult for other neuroimaging techniques.

There are also advantages of ERP over purely behavior measures. For example, reaction time (RT) and accuracy, which are fundamental measures of behavior, are overt responses and may therefore be ambiguous with respect to a specific cognitive operation (Luck, 2005). ERPs, however, are continuous measures of neural activity that are time-locked to the stimulus or the response. It is therefore possible to identify the specific stage in processing that a given variable has its effect. As a second example, ERP allows for the measurement of neural activity when no behavioral response is required (Luck, 2005). For instance, in memory experiments participants often encode to-be-remembered stimuli passively—that is, the only task that participants must perform is attending to the stimuli. In such a behavioral experiment there is no data collection during encoding. In an ERP study, the electrophysiological responses for each stimulus are recorded and thereby available for subsequent analysis.

Lastly, participants' electrophysiological responses to stimuli can often be conditionalized on the basis of stimulus properties (e.g., whether it is a word or a picture, or whether it has been seen before within the context of the experiment). However, they can also be conditionalized on the basis of participants' behavioral responses to the stimuli (e.g., whether it was correctly identified, or whether it was correctly recognized as

seen before). Consequentially, the greater the variety of behavioral responses one collects from participants, the greater the flexibility one has in analyzing and interpreting the electrophysiological data within an information-processing framework (Picton et al., 2005).

The principal disadvantage to ERP is that one cannot unequivocally determine the location of the neural generators that yielded the activity recorded on the scalp; thus, only limited inferences can be made about the likely brain structures responsible for the cognitive processes reflected by ERP. However, recent efforts in this domain have produced source-localization models that seem to generate source-estimates that are fairly consistent with estimates from PET and fMRI. So, although ERP itself will remain poor in terms of its spatial resolution, it may be possible in some instances to derive reasonably accurate *estimates* of neural generator source with source-modeling programs such as *sLORETA* (Pascual-Marqui, 2002).

CHAPTER 4: ERPs IN RECOGNITION MEMORY

It is fair to say that the majority of ERP studies of recognition memory assume a dual-process framework (e.g., Curran, 2000; Düzel, Yonelinas, Mangun, Heinze, & Tulving, 1997; Friedman, 2004; Friedman & Johnson, 2000; Rugg et al., 1998; Rugg & Curran, 2007; Wilding & Rugg, 1996). Thus, most studies focus on specific ERP components associated with either recollection or familiarity to make inferences about these cognitive processes. As will be discussed in the following sections, it appears that there are unique ERP signatures for recollection and familiarity during both intentional memory encoding and during memory retrieval.

Encoding

A large body of evidence provides support for the idea that recollection and familiarity arise from *dissociable neural substrates* (see Aggleton & Brown, 2006; Rugg & Curran, 2007). While the studies supporting this view consist primarily of data collected during retrieval, a reasonable question to ask is whether neural mechanisms operating during encoding may partially constrain the series of processing stages (and processing mechanisms) that operate during retrieval. If so, the neurological activity during encoding may partially determine the phenomenological experience of remembering as well as what one remembers. This possibility raises questions as to whether there are dissociable neural substrates active during encoding that are, themselves, uniquely determinate of later memory. Additional questions are what initiates activity in one neural substrate over the other and to what degree various encoding tasks and encoding strategies influence subsequent memory?

Differences in subsequent memory (Dm): a neural correlate of memory encoding.

With increasing frequency, cognitive neuroscientists are addressing questions

regarding the neural correlates of encoding with the intent to remember. Many of the researchers employ the ERP methodology for the advantages listed at the onset of this chapter and in Chapter 2 (Groh-Bordin, Busch, Herrmann, & Zimmer, 2007; Guo, Zhu, Ding, & Fan, 2003, 2004; Schweinberger & Sommer, 1991; Williamon & Egner, 2004). More specifically, neuroscientists often address questions regarding the neural correlates of encoding by studying “differences in subsequent memory” (Dm; Paller, Kutas, Shimamura, & Squire, 1987), otherwise known as “subsequent memory effects” (Rugg, 1995). To study these effects, researchers record EEG while participants encode a given number of stimuli. While not always the case, encoding is typically passive, with instructions to the observers being only to remember the stimuli for a later memory test. The portion of the EEG corresponding to the duration between stimulus onset and offset (called the EEG epoch) is segregated such that there is a time-locked epoch (generally not exceeding ~2 seconds) for each encoded stimulus. These EEG samples are then segregated once more on the basis of whether or not the corresponding stimuli were remembered during a memory test (as indicated by participants’ behavioral responses during test). This separation of ERP samples enables researchers to compare neural activity at encoding that is correlated with subsequent memory to neural activity at encoding that is associated with subsequent forgetting.

The general finding is that between 400 -1100 ms post-stimulus, subsequently recognized stimuli are associated with more positive-going ERPs during encoding than are subsequently unrecognized stimuli (Figure 4), and this differences is observed along midline electrodes (Fz, Cz, Pz; see Figure 3). Although this effect is for the most part bilaterally distributed, the magnitude of the Dm effect is greatest over the left

hemisphere for verbal stimuli and greatest over the right hemisphere for pictorial stimuli (Friedman & Sutton, 1987).

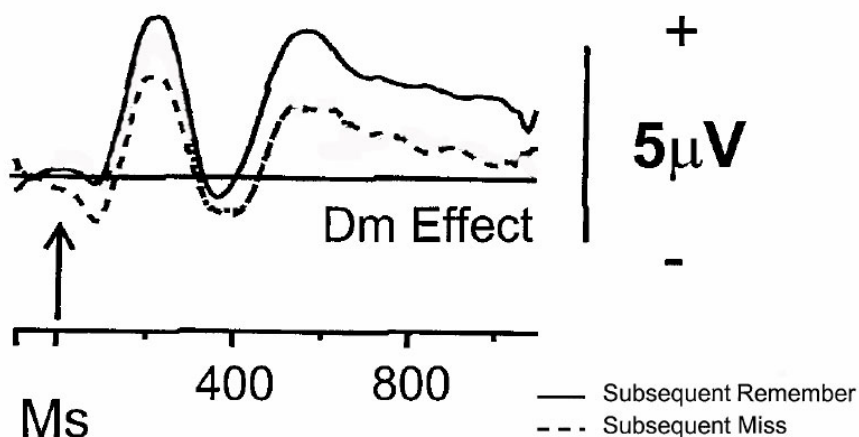


Figure 4. Difference in Subsequent Memory Effect (Dm effect). Figure modified from Johnson & Friedman (2000).

Significance of Dm effects. Compelling support for the implicit-explicit distinction in Dm effects stems from a recent study (Schott, Richardson-Klavehn, Heinze, & Düzel, 2002) in which levels of processing were manipulated (deep vs. shallow). Using this levels of processing task at encoding and a joint word-stem completion task/yes-no recognition task at test, the researchers were able to clearly separate the effects of implicit memory from the effects of explicit remembering. The general procedure was as follows: During encoding, a cue preceded each target word and it indicated whether participants were to rate the pleasantness (deep; semantic task) or count the syllables (shallow; phonemic task) of the target word. Experimenters explicitly instructed the participants not to memorize the words because it would interfere with the rating task. During the test, participants were to complete word-stems with words from the prior list when possible, and with the first word that came to mind

otherwise (inclusion instructions). Participants then gave a yes-no judgment as to whether they had completed the stem with a word from the prior list.

The logic behind this design was as follows: First, prior work (e.g., Craik, Moscovitch, & McDowd 1994) has suggested that phonemic and semantic encoding yield equivalent priming effects and therefore should not lead to differences in word-stem completion performance. The same body of research also showed that explicit memory *does* differ between phonemic and semantic encoding (semantic > phonemic); thus, such a manipulation should affect explicit remembering but not priming. Second, the perceptual representation system (PRS) (a) operates during both perceptual and lexical levels of processing, and (b) temporally precedes conceptual levels of processing (which code to semantic and episodic memory systems); thus, ERP priming effects should be observed at an earlier latency than explicit remembering effects. Also, because phonemic and semantic encoding are known to elicit similar levels of perceptual and lexical processing, and differ only in the level of conceptual processing (Richardson-Klavehn & Gardiner, 1998), Dm effects for remembering items should be based more heavily on activity differences in neural populations associated with conceptual processing than should Dm effects for priming. Thus, the levels of processing manipulation should reveal Dm effects that differ both temporally and topographically.

The results of Schott et al.'s (2002) study justified their logic. Dm effects for words subsequently used to complete the stem via priming emerged around 200 ms and peaked at ~400 ms at midline and parietal electrodes, and (as predicted) there was no effect of the size congruency manipulation on the ERPs for primed words. There was a Dm x size congruency x Electrode interaction for remembered words at parietal

electrodes in the 600-800 ms window (Figure 5a). On the one hand, the Dm effect occurred over left posterior sites in the phonemic encoding condition only. On the other hand, the size congruency effect occurred from 600 ms to the end of the epoch and at fronto-central site (more positive for deep than shallow). With regard to contrasts of the

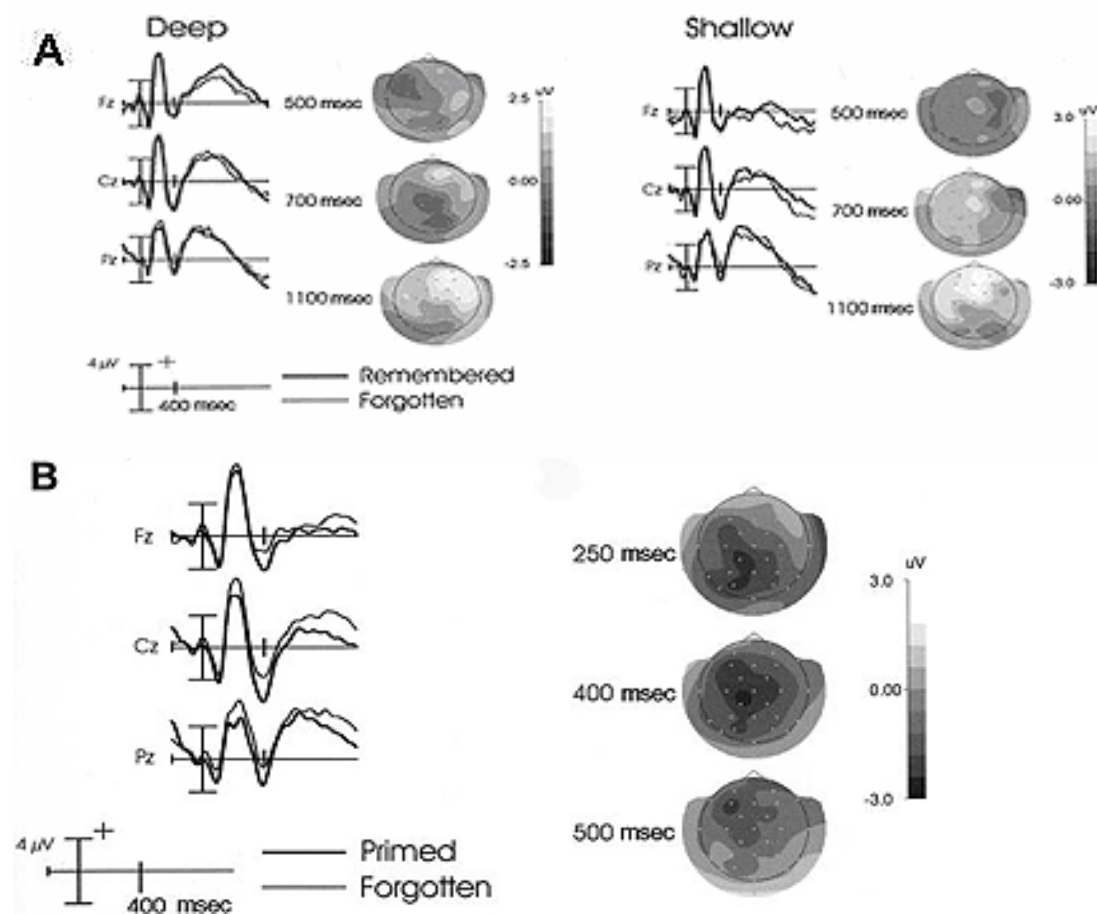


Figure 5. Dm effects in implicit (panel B) and explicit (panel A) memory. Figure taken from Schott et al. (2002).

implicit and explicit Dm effects, the Dm effects did in fact differ temporally (onset between 200-400 ms vs. at 600 ms, respectively) and topographically (midline to parietal vs. left-lateralized posterior, respectively; Figure 5).

The Dm effect in explicit memory may be related to semantic processing, as the effect is often times absent for abstract visual stimuli and inherently meaningless visual

symbols, and reduced in amplitude with decreasing levels of associative and elaborative processing (Wagner, Koustaal, & Schacter, 1999). Some also speculate that the Dm effect may be predictive of subsequent recollection-based recognition, as the amplitude has been observed to decline with decreasing levels of retrieved episodic detail (Friedman & Trott, 2000; Mangles et al., 2000-unpublished). In further support of this idea, the Dm effect is sometimes absent for memory with no contextual retrieval (i.e., familiarity as indexed by “know” responses in the remember-know paradigm; Friedman & Johnson, 2000; Rugg & Curran, 2007).

Although the centro-parietal Dm effect appears not to emerge for acontextual memory, one unpublished report (Mangles et al., 2000) described a second Dm effect observed over the inferior left temporal scalp region (electrode T7) that did not decrease in amplitude with lesser amounts of retrieved context (recalled = “remembered” = “known”). One interpretation of this observation is that this left temporal Dm effect may be predictive of subsequent memory based on familiarity. Unfortunately, there seems to have been no further investigation into this possibility. Future work in this arena should explore this possibility.

Retrieval

As mentioned at the outset of the previous section, most recognition memory ERP studies examine retrieval processes and do so by recording EEG when participants are attempting to discriminate between studied and unstudied stimuli. These studies examine retrieval processes by isolating ERP “old/new effects” (e.g., Warren, 1980). Old/new effects are seen as differences across time in ERP waveforms elicited by repeated (old) versus novel (new) stimuli, with more positive-going waveforms for old than new stimuli being most typical.

The vast majority of studies interpret this retrieval related neural activity within a dual-process framework (see Rugg & Curran, 2007). From this perspective, recognition is supported by a recollection, familiarity, or some combination of the two. While there are various takes on the dual-process framework, there is general agreement that single stimulus recognition can be supported by familiarity alone (although it does not have to be), while associative recognition requires a more detail-rich recollection process.

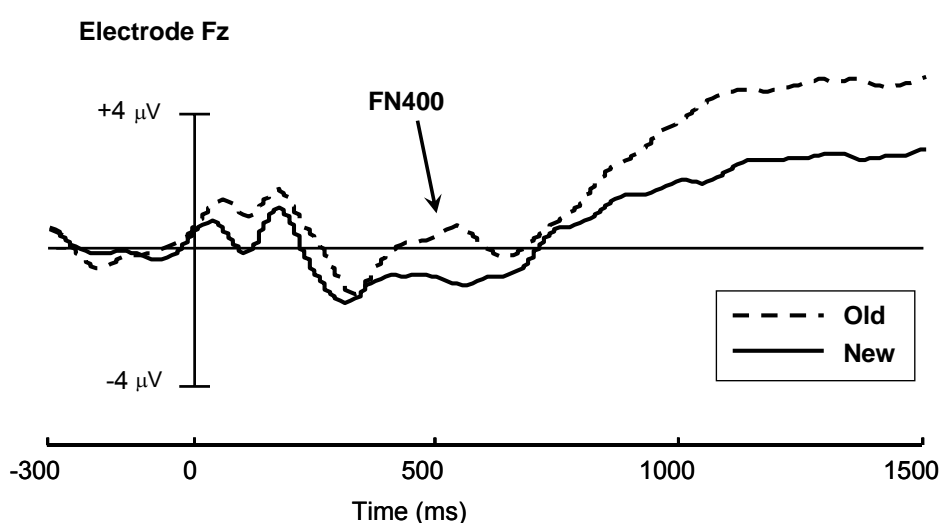


Figure 6. The Mid-Frontal Old/New Effect (FN400). The solid-line waveform corresponds to new items that were correctly rejected, whereas the dashed-line waveform corresponds to old items that were correctly recognized (hits).

Old/New Effects: A Neural Correlate of Successful Memory Retrieval

Two of the most widely reported ERP components in the recognition memory literature are the FN400 (e.g., Curran, 2000), held as a correlate of familiarity (e.g., Curran, 2000, 2004), and the parietal old/new effect (e.g., Curran, 2000; Rugg et al., 1998), which is thought to be a correlate of recollection (for a review, see Curran, Tepe, & Piatt, 2006). It is important to note some also refer to the FN400 as the mid-frontal old/new effect (see Figure 6, Rugg et al., 1998). The following discussion will outline (a)

the characteristics of these ERP components and (b) the degree to which the published research supports the claim that the FN400 and the old/new parietal effects reflect the neural correlates of familiarity and recollection, respectively.

The FN400. The FN400 is characterized by more positive ERPs to old stimuli than to new stimuli over anterior, superior regions (old>new), and with reversed polarity (new>old) over posterior, inferior regions between 300-500 ms post-stimulus. This modulation generally peaks between 400-450 ms post-stimulus and is greatest in magnitude at medial-frontal to fronto-polar sites. Assuming an averaged-reference transformation, this modulation can be verified statistically with a condition (e.g., old, new) by region interaction (e.g., anterior, posterior; Curran, 2000, p. 926-927).

Düzel et al. (1997) and Rugg et al. (1998) were two of the first studies to suggest that the FN400 may be a neural correlate of familiarity. In the Düzel et al. study, they reported distinct scalp topographies with unique time courses for recognition judgments accompanied by “remember” responses versus “know” responses. Know responses, which studies link to familiarity-based recognition in the behavioral literature, were associated with the occurrence of the FN400, whereas remember responses (linked to recollection + familiarity) were associated with both the FN400 and the parietal old/new effect. In the Rugg et al. study, the authors observed a mid-frontal old/new effect that was not affected by depth of processing at encoding (deep vs. shallow), a finding that is consistent with the familiarity hypothesis because familiarity is less sensitive to levels of processing manipulations than is recollection. As in the Düzel et al. study, the mid-frontal old/new effect observed by Rugg et al. dissociated both temporally and topographically from the parietal old/new effect.

Many subsequent studies have approached the investigation of the FN400 in

much the same way as the two aforementioned studies. That is, they sought to manipulate variables with well documented behavioral effects on recollection and familiarity and then examined whether the putative familiarity correlate was modulated in a consistent way. The behavioral literature indicates that familiarity is for the most part insensitive to perceptual mismatching (see Yonelinas, 2002), and has therefore been described as “amodal.”

A popular variable to manipulate in ERP studies of the FN400 has been the degree to which the stimuli match between their study and test presentations. Thus, the common prediction is that the FN400 should be affected very little, if at all, by changes to study-test perceptual mismatching. In general, this is what has been shown. For example, Curran (2000) found similar effects between matching test words and plurality-changed words (PAPER vs. PAPERS). Curran and Cleary (2003) observed similar effects between matching and mirror reversed line-drawings. As Mecklinger (2006) pointed out in his review of ERP measures of familiarity, the fact that changes in perceptual/surface features (Curran et al.) and modality (Curran & Dien, 2003; Nessler et al.) yielded similar ERPs to the ERPs of perceptually-matching stimuli suggests that the familiarity does not operate in only the perceptual domain. Rather, it suggests familiarity processes operate amodally and therefore necessarily includes processing in the conceptual-semantic domain.

Although there is to date a strong case for the FN400’s connection to familiarity-based recognition memory, a small body of research raises valid concerns about the validity of such claims. The strongest of these concerns is voiced by Paller and colleagues (e.g., Paller, Voss, and Boehm, 2007; Yovel & Paller, 2004) who argue that the majority of FN400 research has not successfully ruled out the possibility that the

FN400 is actually a correlate of conceptual priming rather than a correlate of familiarity. For example, they note that familiarity and conceptual priming behave similarly to manipulations of study-test perceptual mismatching (e.g., Curran, 2000; Curran & Cleary, 2003), depth of encoding (Rugg et al., 1998), confidence (Curran, 2004), divided attention (Curran, 2004), and aging (Trott, Friedman, Ritter, Fabiani, & Snodgrass, 1999).

While the aforementioned variables constitute the majority of those used in FN400 research, there are studies to which the conceptual priming argument does not apply. As an example, two separate studies have used stimuli with no inherent meaning (geometric shapes, Curran et al., 2002; unfamiliar faces, Johansson et al., 2004) and still report an FN400 effect. Without preexisting and distinct conceptual representations for the individual experimental stimuli, it is difficult to see how the pattern of neural activity characteristic of the FN400 could be attributed to conceptual processing.

However, stronger evidence of this familiarity-effect's distinction from conceptual priming would be the demonstration their dissociation, which Groh-Bordin et al. (2005) have reported. In their study, participants performed an implicit memory task (living/non-living decision) and a separate explicit memory task with figural stimuli. In the implicit task, repetitions of both the identical stimuli and mirror-reversed stimuli showed equivalent priming in the form of a broad positive slow wave, maximal over the parieto-occipital region between the 500-800 ms window; this effect was not present at frontal electrodes. Conversely, the explicit test elicited a FN400 between 250-450 ms for identical repetitions only; this effect was not present at parietal electrodes. Similar dissociations have also been shown between familiarity and "semantic familiarity" (Nessler, Mecklinger, & Penny, 2005), familiarity and "episodic priming" (Friedman,

2004), and familiarity and “perceptual priming” (Nessler et al.; Rugg et al., 1998) for verbal and non-verbal stimuli. It appears, therefore, that while implicit and explicit memory processes are indeed separable based on their neural correlates, one should ensure that the manipulations used are capable of distinguishing between these different forms of memory.

As stated earlier in this section, familiarity is often described as a process that can be amodal (Curran, 2000)—a state in which perceptual information may be fairly irrelevant compared to conceptual information. However, a few recent studies have suggested that the FN400 may not actually represent a familiarity process that is entirely amodal. For example, Mecklinger et al. (unpublished) manipulated modality at study (spoken words/objects) and tested participants’ recognition with objects. Their design allowed for the contrast of perceptual repetitions (studied objects, object test-cue) with conceptual repetitions (studied words, object test-cue) on the FN400. They observed an early effect (350-450 ms) for perceptual but not conceptual repetitions, and a slightly delayed FN400 effect (450–550 ms) for perceptual and conceptual repetitions. The former effect was equivalent for perceptual and conceptual repetitions at frontal and fronto-polar sites, but it was larger for perceptual repetitions at central sites.

In a study that is also informative with regard to the relative contributions of perceptual and conceptual information to familiarity, Czernochowski, Mecklinger, Johansson, and Brinkmann (2005) presented participants with spoken words or photographs of real-life objects (in different blocks) and tested their memory with line-drawings. Participants were to respond old when the line-drawing denoted a studied stimulus of a particular modality (word or picture), and everything else was to be called new (exclusion task). Overall, targets and non-targets showed an equivalent FN400

(200-400 ms). However, when non-target type was assessed separately, only pictorial non-targets (test pictures studied as pictures to which participants were to respond “new”) elicited an FN400. This FN400 for pictorial non-targets was identical to the FN400 found for word targets (test pictures studied as words to which participants were to respond “old”) and for picture targets; no FN400 was found for word non-targets.

The interesting aspect of this study is that only when the non-targets matched both perceptually and conceptually did an FN400 effect emerge, despite instructions to respond “new” for these stimuli. No FN400 was found when non-targets matched only on the conceptual level. This finding, as well as those of Mecklinger et al. (unpublished) and Groh-Bordin et al. (2005) demonstrate that both perceptual and conceptual processing can drive familiarity based memory judgments. Moreover, the significance of the early onset old/new effect (250 ms) has yet to be clarified. The aforementioned ERP studies concerning possible perceptual and conceptual modulations of the FN400 bear directly on the theoretical motivations behind the experiments of this dissertation. As such, they are discussed within this context in later sections (Chapter 6).

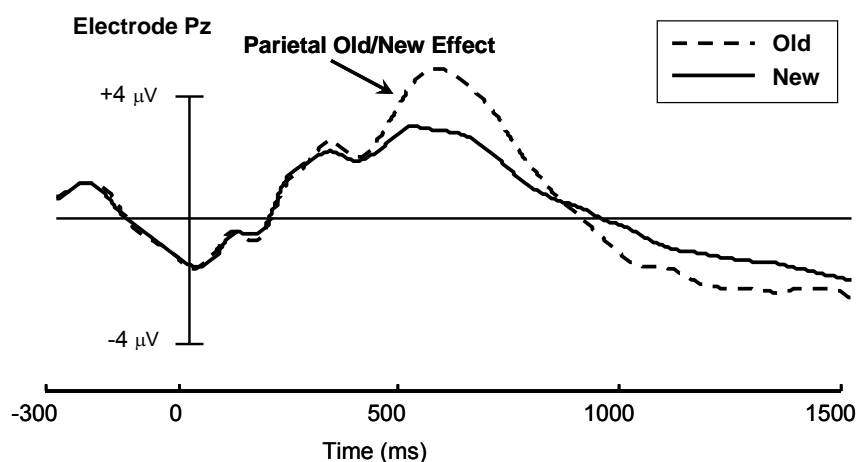


Figure 7. The Parietal Old/New Effect. The solid-line waveform corresponds to new items that were correctly rejected, whereas the dashed-line waveform corresponds to old items that were correctly recognized (hits).

The parietal old/new effect. The parietal old/new effect (Figure 7) represents a more positive going waveform for correctly endorsed old stimuli relative to correctly rejected new stimuli between 400-800 ms post stimulus (e.g., Donaldson & Rugg, 1998; Wilding et al., 1995). As described by Curran (2000, p. 927), the effect is "...a greater voltage difference between posterior, superior and anterior, inferior regions for old stimuli than for new stimuli." Like the FN400, the effect is also statistically indicated by condition X region interactions. This effect is generally maximal over left temporo-parietal regions and is usually larger over the left than the right hemisphere, but this is not always the case (e.g., in continuous recognition procedures, Van Strien, Hagenbeek, Stam, Rombouts, & Barkhof, 2005). The effect generally onsets around 420-490 ms, peaks at ~550-600 ms, and offsets around ~790-800 ms.

The general consensus is that the parietal old/new effect is a likely neural correlate of recollection. The evidence supporting this assertion comes from the many studies demonstrating that the parietal old/new effect is modulated by the same variables thought to influence behavioral measures of recollection. For example, the effect has been shown to be largest for consciously remembered stimuli and absent for misses and false alarms (Smith 1993; Wilding, Doyle, & Rugg; 1995); this is consistent with predictions from behavioral research because, in theory, one should not show neural correlates of recollection for stimuli that were not explicitly remembered (misses), nor for stimuli "recognized" but nevertheless unstudied (false alarms).

Other examples of consistency between behavioral and ERP measures include demonstrations that the old/new effect is sensitive to size congruency manipulations (Paller & Kutas, 1992), and larger ERP old/new differences occur when recognition is

accompanied by recall (Rugg et al., 1996) or accompanied by retrieval of context or some type of source specifying information (e.g., list membership; Trott et al., 1999). The parietal old/new effect is also consistently larger for recognition accompanied by the phenomenological experience of recollection (“remember” judgments) versus the phenomenological experience of familiarity (“know” judgments; Trott et al.). Moreover, Johnson (1995) and others (e.g., Düzel et al., 2001; Smith & Halgren, 1989) have shown that the parietal old/new effect is absent in patients with damage to areas of the brain hypothesized as critical to recollection (e.g., lesions to medial temporal lobe, bilateral hippocampal damage).

A challenge to the assertion that the parietal old/new effect reflects recollection comes from studies contrasting recollection occurring with and without the retrieval of the encoding context/source. The logic in such studies has been as follows: If the parietal old/new effect actually reflects recollection (which is assumed to involve the retrieval of encoding context), and if recollection processes are functionally and anatomically distinct from acontextual familiarity processes, then recognition memory accompanied by context retrieval should show a pattern of neural activity that is *qualitatively* distinct from recognition not accompanied by context retrieval (i.e., familiarity). Contrary to this logic, however, the prevalent finding is that recognition with and without context does not produce topographically distinct patterns of neural activity at the scalp (e.g., Trott et al., 1999; Wilding, Doyle, & Rugg, 1995; Wilding & Rugg, 1996). Rather, equivalent or amplitude-attenuated old/new effects were observed between high-contextual and low-contextual recognition. This finding is fairly consistent, and one interpretation is that because the parietal old/new effect cannot dissociate contextual and acontextual recognition, it cannot be a neural correlate of recollection

and therefore cannot be used as evidence in support of dual-process theory in recognition memory (e.g., Wilding et al., 1995, 1996).

An alternative interpretation is that recollection is a graded phenomenon that is sensitive to the amount of contextual information retrieved (Wilding, 2000). From this perspective, if the parietal old/new effect was assumed to reflect a graded recollection process, contrasts of scalp distributions at varying degrees of context retrieval would not be expected to yield qualitative/topographic differences. This line of reasoning leads some to argue that in order to demonstrate qualitative differences between the neural correlates of recollection and familiarity (and find support for dual-process theory), one should contrast scalp distributions of the FN400 and the parietal old/new effects (see Friedman, 2004). Although this practice presupposes that the parietal and FN400 old/new effects are indeed correlates of recollection and familiarity, respectively, the ERP literature reviewed in this and the preceding section makes a strong case for this presupposition. Moreover, the evidence from the functional imaging literature is highly consistent with the evidence from ERP studies (see Rugg & Yonelinas, 2003). It therefore seems likely that the easily dissociable FN400 and parietal old/new effects provide a convenient means of further studying dual-process recognition. This dissertation seeks to assess how manipulations of perceptual and conceptual processing modulate the FN400 and parietal old/new effects as a method for further understanding the nature of recollection- and familiarity-based recognition.

Priming ERP effects and recognition memory. Besides the hypothesized recollection and familiarity processes involved in recognition, there are other processes believed to contribute to recognition that have, themselves, been linked to distinct patterns of neural activity. One such process is implicit in nature and the other process

concerns activity that occurs after the retrieval attempt. As discussed in earlier sections, some theories of recognition describe familiarity as relying to various degrees on implicit memory or “fluency” (e.g., Tulving, 1985; Whittlesea & Williams, 2000, 2001).

The ERP literature credits Rugg et al. (1998) as the first in demonstrating a clear neural correlate of priming that was unequivocally dissociable from the neural correlates of recognition memory. In this study, Rugg and his colleagues examined the dynamics of participants’ memory for words under deep and shallow encoding condition. For those words that participants studied under shallow encoding conditions, only ~50% were correctly recognized. The large proportion of unrecognized study-list words allowed Rugg to examine whether these unrecognized words still demonstrated an “old/new” effect. Upon inspection, Rugg et al. observed that old, unrecognized words elicited waveforms that were reliably greater than new, correctly rejected words across the 300-500 ms post-stimulus duration. This effect was only present at posterior scalp regions and showed hemispheric asymmetry such that it was somewhat right-lateralized over the parieto-occipital region. The old/new effect was shown as qualitatively different from a second effect found for recognized, shallowly encoded words within the same time window (300-500 ms; the FN400). Qualitative differences imply that the neural populations eliciting the activity are at the very least partially non-overlapping; the presumption being that distinct neural populations imply somewhat distinct neural processes (although they could both contribute to the same cognitive operation).

The argument has been made that familiarity is actually based on fluency attributions (Whittlesea & Williams, 2001) or some other implicit process (perceptual or conceptual), or at the very least that implicit processes play a large role in familiarity. Within the ERP literature some have argued that the FN400 itself may actually be a

correlate of an implicit process (Voss and colleagues, Paller, Voss, & Boehm, 2007; Voss & Paller, 2007, 2008; Voss, Reber, Mesulam, Parrish, & Paller, 2008). It has therefore been of great theoretical interest that Rugg et al. (1998) have shown a dissociation between a neural correlate of familiarity and a possible neural correlate of implicit memory. Rugg et al. showed that old/new differences between unrecognized words (words for which there was no behaviorally measurable explicit memory) and new words produced a distinct scalp topography from that of old/new differences between recognized words (words for which there was behaviorally measurable explicit memory) and new words. Moreover, the magnitude of the effects were equivalent, demonstrating that the effect between unrecognized words and new words was not merely a neural correlate of weak explicit memory. Rugg et al.'s study is generally viewed as diagnostic evidence for the existence of a distinct neural process associated with implicit memory. Other studies have demonstrated similar effects which have been consistently observed over specific regions of the scalp (right lateralized occipito-temporal, parieto-occipital; e.g., Friedman, 2004; Johnson et al., 1998; Paller & Gross, 1998).

CHAPTER 5: IDENTIFYING THE CONTRIBUTION OF PERCEPTUAL AND CONCEPTUAL PROCESSES TO FAMILIARITY WITH ERP

Recent ERP studies manipulating perceptual and conceptual processing in recognition memory have demonstrated that qualitatively different types of information can support both recollection-based and familiarity-based recognition (e.g., Ecker & Zimmer, 2009; Ecker, Zimmer, & Groh-Bordin, 2007; Groh-Bordin et al., 2006; Grove & Wilding, in press; Schloerscheidt & Rugg, 2004; Srinivas & Verfaellie, 2000). However, much of this work is silent on more specific issues, such as the nature of the perceptual and conceptual memory representations involved in recollection and familiarity, and how these representations interact with the various attributes of retrieval cues to elicit recollection and familiarity.

In developing an approach for confronting these questions, the considerations are as much about how the retrieval cue is processed and in what manner it accesses a given memory trace, as they are about how the initial stimulus is processed and which of its attributes are stored in the memory trace. The recognition memory ERP literature pertaining to memory retrieval and perceptual and conceptual information processing is an asset to understanding what may be stored in the memory trace. The relatively meager recognition memory ERP literature pertaining to both the neural correlates of encoding and the influence of perceptual and conceptual processing is somewhat of an obstacle. However, in research one can occasionally gain considerable insight into a particular issue by considering work from a related or analogous field. In what follows, Chapter 5 describes ERP research from the field of object identification and how it may be able to speak to the issues of central interest to this dissertation.

Linking Object Identification and Object Recognition Memory?

Perceptual closure is one of the many neural processes by which the brain comes to identify images of fragmented or partially occluded objects in the natural world (Bartlett, 1916; Snodgrass & Feenan, 1990). The term “perceptual closure” refers to the neural interpolation of missing or obstructed visual information from the visual information that *is* available. The closure process uses the estimated missing/obstructed visual information to complete the object’s visual structure, enabling subsequent perceptual and semantic processes to determine object identity.

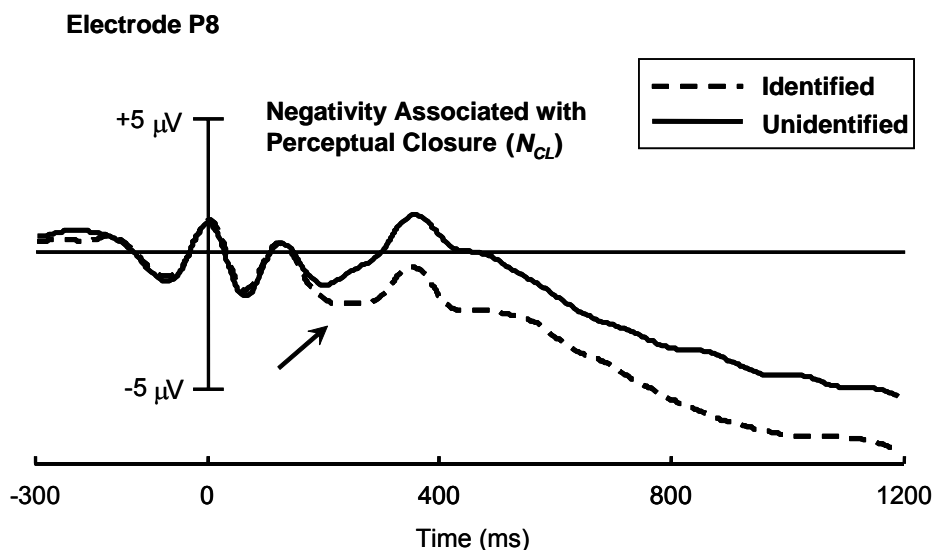


Figure 8. The Negativity Associated with Perceptual Closure (N_{CL}). The solid-line waveform corresponds to items that were not identified by name during encoding, whereas the dashed-line waveform corresponds to items that were identified by name during encoding.

Electrophysiological research has identified a component that is closely tied to the perceptual closure stage of object identification. This component is the N_{CL} , so called because it is seen as a more negative-going waveform for objects that have achieved perceptual closure relative to those that have not (Figure 8). The N_{CL} occurs 230-400 ms post-stimulus, is maximal around 290-300 ms, and is present over bilateral

occipito-temporal scalp regions (e.g., electrodes PO5/PO6; Doniger et al., 2000; Sehatpour, Molholm, Javitt, & Foxe, 2006). The N_{cl} is not linked to object identification itself, but rather to the extraction of object information under circumstances in which the object is difficult to identify (e.g., fragmented, masked). According to Sehatpour et al.'s (2006) model, the N_{cl} reflects effortful processing on a conceptual level and begins only after earlier automatic perceptual processes (reflected by the P1 and N1 components) fail to identify an object.

There does, however, appear to be an ERP component closely correlated with object identification itself: The N350 (Figure 9). The N350 component is so named because the waveform associated with unidentifiable objects is more negative-going than the waveform associated with identifiable objects, maximally between 325-400 ms along frontal, midline electrodes (e.g., Fz). Studies of the N350 demonstrate the earliest known separation of waveforms for identifiable and unidentifiable objects, which beings around 300ms post-stimulus (e.g., Pietrowsky et al., 1996). The current view is that the onset of the N350 effect marks the upper temporal bounds of correct object model/representation selection from long-term memory (Schendan & Kutas, 2002, 2007a, b).

According to Schendan and Kutas (2002, 2007b), the N350 corresponds to a search of the structural description system (Schacter, 1994) for a perceptually matching structural representation of the object being viewed. The structural description system itself abstractly represents the global structure of objects and their component parts, such that global object shapes are retained in the absence of more detailed object features contained within episodic representations, such as size and spatial location and orientation (e.g., Biederman & Cooper, 1991a). The information stored in the structural

description system is, "...a kind of *generic memory*, that is, explicit memory which is not episodic, such as for recognition and recall tasks, but rather for semantic or nonsemantic (i.e., perceptual) information or facts, regardless of a temporal event context" (Schendan & Kutas, 2003, p. 745). A successful match between the percept and such a representation in the structural description system allows object categorization to occur and for subsequent processes that, too, contribute to eventual object naming.

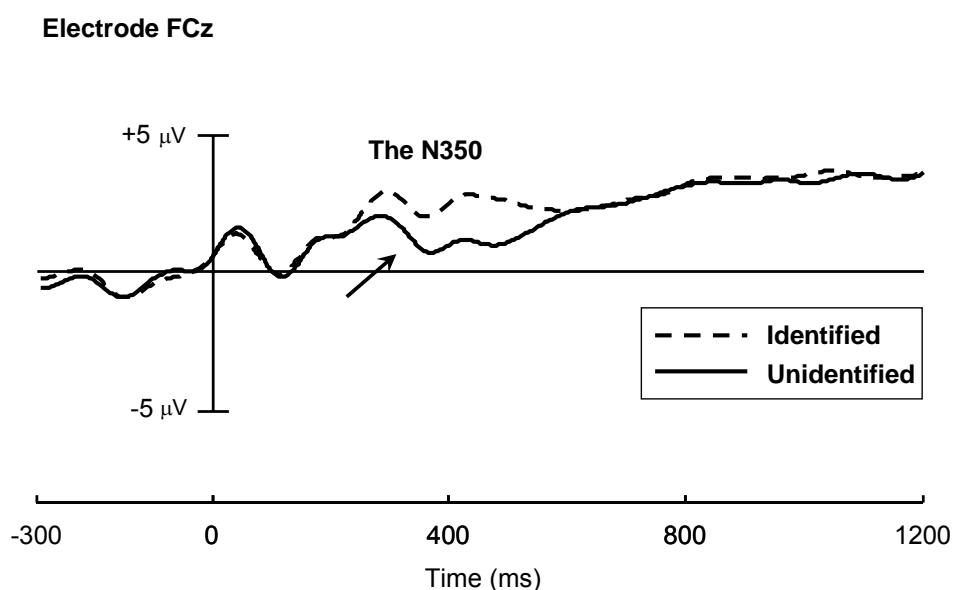


Figure 9. The N350. The solid-line waveform corresponds to items that were not identified by name during encoding, whereas the dashed-line waveform corresponds to items that *were* identified by name during encoding.

The Schendan and Kutas (2002, 2007a, b) model of object identification predicts that the N350 will be large when the recovered object components match many structural object descriptions stored in memory (either because the recovered object components are few or simply non-diagnostic), resulting in a long, but ultimately unsuccessful, search. Conversely, the N350 will be smaller when a successful structural description match is made that leads to identification, or when too little visual

information is available for matching at any level to occur. Repetition (new>repeated), perceptual expertise (unusual>canonical views), and object viewpoint (different>same) also modulate the N350, and do so in a manner that is consistent with the idea that the component indexes an object structure search within a system containing abstract perceptual representations (i.e., the structural description system).

It seems likely that the perceptual information used to conduct an object model search is a product of the perceptual closure process (that is, under conditions in which the perceptual closure processes is needed in the first place; Schendan & Kutas, 2007b). Thus, it would stand to reason that if the perceptual closure processes were unsuccessful for a given stimulus, then object model selection would also be unsuccessful (or at least difficult) for that stimulus because the search would be based on incomplete perceptual information. As is discussed in Chapter 6, the known relationship between perceptual closure (N_{CL}) and object model selection (N350) may allow for novel predictions to be made about nature of explicit recognition memory for pictures that are difficult to identify.

Characterizing how and when the brain uses visual information to determine object identity is important in its own right. It is also important because it may inform the understanding of the higher-order cognitive operations that act upon (or those that depend exclusively upon) the outcome of identification processes, such as object model selection. Indeed, some researchers have examined the neural mechanisms underlying object identification and their relationship to higher-order mental processes, such as *memory*. However, the majority of such studies have only examined the relationship between object identification processes and implicit memory (e.g., Schendan & Kutas, 2002, 2003, 2007a, b). Of the studies that have examined the neural underpinnings of

explicit memory for pictorial and object information, most have done so with respect to retrieval processes exclusively (Ecker & Zimmer, 2009; Ally & Budson, 2007; Alley et al., 2008).

Behavioral research in this domain has led to predictions about the relative timing of the neural events necessary for object identification and object recognition (Subramaniam, Biederman, & Madigan, 2000), although empirical data have not yet confirmed these predictions. Specifically, Subramaniam et al. tested participants' recognition memory for 90 line drawings in a rapid serial visual presentation (RSVP) stream. The participants viewed the individual RSVP pictures at one of five durations (72, 126, 196, 462, or 700 ms). Immediately following the RSVP stream, participants completed a two-alternative forced-choice (2AFC) recognition test for all RSVP drawings. The picture pairs on each test trial were a target with either (a) an exemplar foil (visually similar, but verbally identical), (b) a visually and verbally distinct foil, or (c) a visually and verbally distinct foil but with the target itself being mirror-reversed. Memory performance for all test-trial types was at chance for the 72 and 126 ms presentation rates. For the three slower presentation rates, recognition was above chance and increased reliably with increasing presentation durations; picture recognition did not differ as a function of the similarity of the target or the foil to previously presented pictures.

Although it is somewhat surprising that Subramaniam et al. (2000) did not find attenuated recognition memory performance for mirror-reversed-target test-trials, as is typically the case (e.g., Biederman & Cooper, 1991, Curran & Cleary, 2003), there is precedent for this outcome. In a similar experiment, Intraub (1980) found no effect of mirror-reversed targets on recognition following encoding via RSVP. Together with

other data from their study showing poor identification performance and a lack of picture priming (when the prime itself was presented in the RSVP stream) during 72-126 ms presentation rates, Subramaniam et al. argued that while 50-100 ms of uninterrupted neural activation in inferotemporal (IT) cortex is sufficient for object identification, it is not sufficient for subsequent picture priming and recognition memory.

Single-cell recordings of macaque IT neurons (Tovee & Rolls, 1995) support Subramaniam et al.'s (2000) argument by showing that much of the information stored in IT cells that respond selectively to objects or object parts is acquired within the first 50 ms of activation (e.g., Takana, 1996). Of particular importance to their case is that despite requiring a mere 50 ms to derive the information necessary for object identification, IT cells continue to fire for an additional 350 ms minimally (e.g., Logothetis & Sheinberg, 1996). Subramaniam et al. argue that the additional neural activity (which they term "post-perceptual activity") is critical for the instantiation of a stable object representation. They explain the lack of perceptual priming and recognition memory for short duration RSVP pictures (despite reasonable identification) by positing that the rapid onset of the pictures in the RSVP stream directs attention from picture to picture, and that this rapid shifting of attention disrupts/suppresses the critical post-perceptual activity. At longer durations (+200 ms), post-perceptual activity can engage long enough to develop more lasting object representations before being suppressed by the onset of the next RSVP stream picture. This argument is also consistent with Subramaniam et al.'s data in that above chance identification, but not priming or recognition memory, is apparent at durations under 200 ms, whereas subsequent visual priming and recognition memory are only apparent at durations exceeding 200 ms.

The relative paucity of research on the relationship between the initial encoding

of pictorial/object information, the role of well characterized object identification processes, and subsequent explicit memory in part motivates the approach of the experiments described in this dissertation. As an initial attempt to link what is known about the ERP correlates of object identification to object recognition memory, the present approach is similar to the approaches taken in prior electrophysiological studies of object identification that have used fragmented images (e.g., Doniger et al., 2000) and object identification and implicit memory (e.g., Schendan & Kutas, 2002). In the present study, however, black and white line drawings were presented briefly and forward and backward masked in an attempt to hinder identification. Pictures that are not identified can be analyzed separately from those pictures that are identified. Furthermore, the data can be further divided on the basis of whether the pictures in the identification task (encoding) are recognized on a subsequent test of memory.

The rationale for the parsing of data on the basis of subsequent memory is that it will allow for a direct assessment of the relationship between the identification processes during encoding and their potential influences on memory. Specifically, what is known about the aforementioned object identification related ERP components (N350, N_{CL}) may be informative with regard to the type of processing that may or may not be necessary for successful subsequent memory. That is, searching for the presence/absence of ERP components with known links to specific types of processing and neural representations may be informative when contrasting memory for identified and unidentified pictures. Moreover, the presence/absence of these components may provide clues to the type of pictorial information stored for pictorial information. The more that is known about the information stored within the memory traces, the more that is known about the type of evidence capable of supporting familiarity-based memory.

CHAPTER 6: EXPERIMENT 1

Rational and Justification

The central question motivating this dissertation is: *What type of information can serve as “evidence” for familiarity-based memory?* With regard to this question, the previous chapters have identified (a) why the question is important, (b) methodologies for addressing the question, and (c) the contributions that could come from a study examining this question. These points are summarized and then expanded upon here.

As described in Chapter 2, this question is theoretically important because prominent models of recognition memory assume a familiarity process that is based on the strength of available *evidence* but fail to specify the nature of the evidence (Wixted, 2007a, b; Yonelinas, 1994; Yonelinas & Parks, 2007). The long-term usefulness of a memory model depends on its ability to continue to predict memory performance under new circumstances and to guide research toward further specifying how the memory process operates—this includes providing specificity on the type of information supporting the memory process. It is the latter point that proves difficult for existing models.

Also described in Chapter 2 is the substantial behavioral data suggesting that familiarity can rely on the perceptual and/or the conceptual attributes of stimuli. However, from these data it is still unclear why in some instances familiarity appears to rely primarily on perceptual evidence and in other instances on conceptual evidence. Such ambiguity makes it difficult to address more specific questions concerning the specific types of perceptual (or conceptual) information that may support familiarity.

Chapter 4 describes ERP studies of recognition memory that have been especially useful in characterizing familiarity, recollection, and their contribution to

recognition memory at the neural level. Compared to behavioral methods, the ERP method has the advantage of providing extraordinary amounts of *useful* data during memory encoding, whereas in behavior methods there is typically little to none. Relatively few studies have exploited this advantage, however. At present, an entirely open question is whether manipulations of perceptual and conceptual processing at encoding will have selective effects on the neural correlates of recollection and familiarity.

Chapter 5 describes how the obstacle of a limited literature on the neural correlates of memory encoding can be circumvented by turning to the literature on the neural correlates of object identification. The ERP object identification ERP literature reports on several electrophysiological markers of visual object processing, which I have argued can be used to assess the perceptual/conceptual processing stages that must occur for a picture to be recognized on a later memory test. Ultimately, turning to the object identification literature to make predictions should allow for the experiments presented in this dissertation to help close the gap in the ERP memory literature by producing data directly pertaining to perceptual/conceptual processing during memory encoding.

Experiment 1 was designed to examine the neural correlates of encoding and retrieval together. This approach may be particularly informative because, unlike many studies that address issues of encoding and retrieval separately, the two data sets here come from the same participants, come from the same experimental procedure, and thus have direct bearing on one another. Relative to studies examining either encoding or retrieval in a single study, the present design may allow for stronger and more direct inferences to be made between the encoding and retrieval data.

A unique theoretical element of this study is its approach to examining the neural correlates of encoding and subsequent memory. In particular, the present study seeks to utilize what is known about the temporal dynamics of processes involved in object identification to guide the examination of processes of object encoding that are critical to subsequent object recognition memory. The relative paucity of research on the relationship between the initial encoding of pictorial/object information, the role of well characterized object identification processes, and subsequent explicit memory in part motivated this line of research.

As an initial attempt to link what is known about the ERP correlates of object identification to object recognition memory, the approach of the present investigation is similar to the approaches taken in prior ERP studies of object identification (e.g., Doniger et al., 2000) and prior ERP studies of object identification and its relationship to implicit memory (e.g., Schendan & Kutas, 2002). As discussed in Chapter 5, most studies examining identified versus unidentified objects have used fragmented images. In Experiment 1, however, black and white line drawings were presented briefly and forward and backward masked in an attempt to hinder identification. Those pictures that were not identified can be analyzed separately from those pictures that are identified. Furthermore, the data were further divided on the basis of whether the pictures in the identification task (encoding) were recognized on a subsequent test of memory. The rationale for this parsing of data on the basis of subsequent memory was that it allowed for a direct assessment of the relationship between the identification processes during encoding and their influences on memory. Specifically, what is known about the aforementioned object identification related ERP components (N350, N_{CL}) may be informative with regard to the type of processing that may or may not support

subsequent memory. That is, searching for the presence/absence of ERP components with known links to specific types of processing and neural representations may be informative when contrasting memory for identified and unidentified pictures.

Experiment 1 was also designed to engage recollection- and familiarity-based recognition processes. Under these conditions, their putative neural correlates can be manipulated, recorded, and evaluated. The attributes of the resulting ERPs may speak to the nature of recollection and familiarity as retrieval processes. In particular, the present study was concerned with the effects of encoding, perceptual matching between study and test stimuli, and the interaction of these factors with measures of recollection and familiarity based memory. Levels of processing (or depth of encoding) is a well studied manipulation in ERP studies of memory (e.g., Otten, Henson, & Rugg, 2001; Otten & Rugg, 2001; Rugg, Allan, & Birch, 2000; Rugg et al., 1998; Sanquist, Rohrbaugh, Syndulko, & Lindsley, 1980), and has been consistently shown to dissociate ERP correlates of recollection and familiarity. Perceptual matching is another well studied manipulation (e.g., Curran & Cleary, 2003; Curran & Dien, 2003; Ecker & Zimmer, 2009; Ecker, Zimmer, & Groh-Bordin, 2007; Groh-Bordin, Zimmer, & Ecker, 2006; Grove & Wilding, in press; Schloerscheidt & Rugg, 2004; Srinivas & Verfaellie, 2000), the use of which, however, has lead to several inconsistencies (particularly with respect to its effect on familiarity), and thus warrants further examination.

Typically, ERP studies examining recollection and familiarity employ the remember-know procedure (e.g., Diana, Vilberg, & Reder, 2005; Duarte et al., 2004; Düzel et al., 1997; Spencer, Vila Abad, & Donchin, 2000; Trott et al, 1999; Vilberg, Moosavi, & Rugg; 2006; Wolk et al., 2006, Wolk et al., 2007). However, data from the remember-know procedure are difficult to interpret in light of recent studies suggesting

that “remember” and “know” judgments may actually measure different degrees of recollection rather than recollection and familiarity, respectively (e.g., Wais et al., 2008). Thus, the present study employed a variant (Langley, 2008; Langley & Cleary, 2008) of the recognition without perceptual identification procedure (RWPI; Cleary & Greene, 2004; Langley et al., 2008), which has proven useful in previous studies for separating familiarity-based recognition from recognition based on both recollection and familiarity. Because this procedure had yet to be used in an ERP study, the resultant behavioral and electrophysiological data were contrasted with a “standard” recognition memory procedure run in a within-subjects design. Doing so allowed for an assessment of the generalizability of the data emerging from the recognition without identification procedure (RWI; Peynircioglu, 1990; Cleary & Greene, 2000) thus making the data more readily interpretable within the context of past research.

The present procedure was a hybrid of the RWPI procedure (Cleary & Greene, 2005; Langley, et al. 2008) and the impoverished encoding procedure used by Gregg and Gardiner (1994). In the case of Langley et al., participants studied a series of pictures for a subsequent recognition test. During retrieval, all test pictures were forward and backward masked and presented for 60ms. Participants attempted to identify each test picture and then, regardless of their success, rated the likelihood (on a scale of 0-10) that the briefly presented pictures were previously encoded during study. The authors observed that participants were able to discriminate between studied and unstudied pictures that could not be identified by name during retrieval. Such successful RWPI at retrieval replicated one previous study using verbal stimuli (Cleary & Greene, 2005), and helped to further extend the original RWI effects found using word fragmentation as the means of hindering identification (e.g., Cleary & Greene, 2000;

Peynircioglu, 1990). Data from this procedure converge on the idea that recognition memory for stimuli not identified either at encoding or retrieval is largely familiarity-based.

In line with the logic of Gardiner and Gregg (p. 475, 1997), it is presumed here that by having participants encode stimuli under impoverished conditions that researchers are “minimizing the possibility of encoding stimuli in any distinctive way,” which, based on the understanding of recollection’s reliance on the retrieval of distinctive stimulus features (Hunt & McDaniel, 1993; Rajaram, 1998) should also minimize the possibility of a participant subsequently recollecting the stimulus during testing. A key assumption of the RWPI at encoding procedure, therefore, is that if a stimulus cannot be identified during the perceptual identification task at study, it is unlikely for it to be fully recalled or recollected at test. It is important to note, however, that there is always the possibility that participants may experience “non-criterial recollection” (or “partial recollection”), in which an aspect of the brief pictorial episode is retrieved but fails to lead to the complete recollection and retroactive identification of the picture.

Given the criticisms of the remember-know and process-dissociation behavioral procedures, and ROC analysis as a method for determining the contribution of recollection, there does not appear to be a single reliable means of using behavioral data to rule out the potential contribution of recollection to the recognition of pictures unidentified at encoding. Therefore, a question of interest (addressed in Experiment 1) was whether the putative neural correlates of both recollection and familiarity are present for unidentified pictures. If recollection does contribute to the recognition of unidentified pictures, then an FN400 old/new effect (correlate of familiarity) *and* a

parietal old/new effect (correlate of recollection) should be observed during retrieval. If recognition of unidentified pictures is in fact based largely on familiarity, as would seem to be the case, then only an FN400 old/new effect should be observed during retrieval. If the former pattern is found, there would be stronger justification for examining the RWPI at encoding effect under conditions thought to modulate perceptual and conceptual processing (Experiment 2).

Assuming that only an FN400 old/new effect is found for unidentified pictures at retrieval (a result that would imply familiarity), then identifying the encoding processes unique to recognized but unidentified pictures may be a first step toward assessing potential contributions of underlying perceptual and conceptual processes. The object identification literature has established the time courses during which perceptual and conceptual processes operate in functional isolation and in parallel. Thus, it is largely the timing of the neurophysiology identified as unique to recognized but unidentified pictures that could expose any specific role of perceptual or conceptual processing. Thus, the goals of Experiment 1 were to (a) determine whether an FN400 would be present for unidentified pictures in the absence of a parietal old/new effect and (b) identify any neural correlates of object identification processes that distinguish recognized unidentified pictures from recognized identified pictures and forgotten pictures.

Predictions

The primary predictions regarding the ERP data are as follows. During encoding, it is predicted that only identified pictures will undergo perceptual closure (N_{CL}), and thus will also only elicit an N350. Dm effects are highly inconsistent and may not be present under these circumstances. If a Dm effect is present, it is predicted that it would

be present for identified pictures. With regard to retrieval, it is predicted that identified pictures will elicit an FN400 and a parietal old/new effect, whereas unidentified pictures will elicit only an FN400.

Method

Participants

Thirty-two Iowa State University undergraduates participated in exchange for research participation credit in a lower-level psychology course. All participants provided informed consent, and the study was approved by the Human Participant Institutional Review Board of Iowa State University.

Materials

Stimuli were 640 line drawings, 320 of which were mirror-reversals of the original 320. The original 320 line drawings were obtained from the International Picture Naming Project database (Szekely et al., 2004) among other sources. Stimuli were divided into four 80-trial blocks. For each 80-trial block, there were 40 trials of drawings from the original set and 40 from the mirror-reversed set. Stimuli were counterbalanced across block and drawing set type. During encoding, the stimuli were forward and backward masked with a mask used in prior studies (e.g., Langley et al., 2008). The mask consisted of black, curved lines extending in all directions (scribbles) on a white background (Figure 10).

Procedure

The following describes the procedure of Experiment 1, in which the relative ease of encoding was varied between two tasks. During retrieval, the same manipulation occurred across both tasks. Specifically, the perceptual match (matching pictures vs. mirror reversed pictures) of old test pictures was manipulated between study and test.

Participants completed four study-test blocks, each consisting of 45 encoding trials and 90 test trials. The study-test blocks differed only in stimulus presentation duration during encoding, hereafter referred to as short (33 ms) and long (500 ms) encoding conditions. Participants completed two study-test blocks of each condition.

Encoding. As illustrated in Figure 10, encoding trials lasted 2100 ms, beginning with a 500 ms fixation ‘+’. The forward mask (100 ms), pictorial stimulus (33 ms or 500 ms), and the backward mask (100 ms) were presented in succession with no ISI between presentations. The backward mask was followed by a blank screen (short = 1367 or long = 900 ms). Following this 2100 ms encoding trial, a ‘?’ appeared, prompting participants to name the drawing aloud. Participants were encouraged not to withhold unconfident responses, but were also cautioned not to guess. Rather than offering a blind guess, participants were instructed to respond with “I don’t know.” After the experimenter recorded naming accuracy, a 1000 ms blank was followed by the onset of the next encoding trial.

Retrieval. Each retrieval trial lasted 2000 ms, beginning with a 300 ms fixation ‘+’. One of three types of stimuli followed the fixation for 1500 ms. Test stimuli were either *new* (1/2), *reversed-old* (1/4), or *same-old* (1/4). All test stimuli were followed by a 200 ms blank, which was followed by a ‘?’ that prompted participants to make an old/new recognition judgment on an 6-point rating scale (OLD 1 2 3 | 4 5 6 NEW), with “1” indicating highest confidence old (“3” lowest) and with “6” indicating highest confidence new (“4” lowest). A 500 ms blank followed the participants’ response, which was itself followed by the onset of the next test trial. Participants were instructed to endorse mirror-reversed stimuli as old (inclusion instructions).

SHORT ENCODING

LONG ENCODING

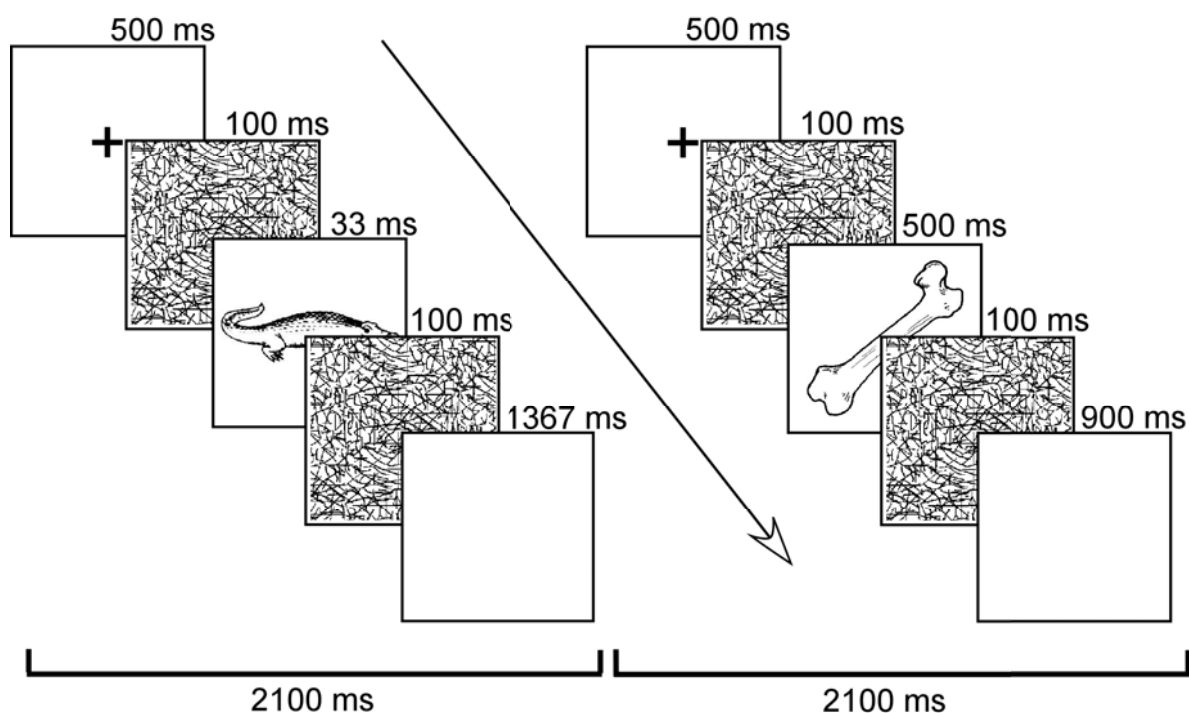


Figure 10. Encoding Procedure for Experiment 1.

To prevent participants from developing encoding strategies based on prior knowledge of the two unique encoding conditions, participants were not informed about the specifics of a given encoding condition until its onset. Participants completed two blocks of one condition before being introduced to the other. This blocking regiment ensured that participants could not accurately anticipate or prepare for the third or fourth block during the previous two. Moreover, this blocking regiment made it more likely that the potential practice effects across blocks one and two would be similar to the potential practice effects across blocks three and four. Counterbalancing dictated the assignment of stimuli set (original vs. mirror-reversed) to encoding condition (short vs. long) and block (one, two vs. three, four).

Electrophysiological recording and preprocessing. An array of 68 scalp electrodes (*Fpz, Fz, FCz, CPz, Pz, POz, Oz, Iz, Fp1, Fp2, Af3, Af4, F1, F2, F3, F4, F5, F6, F7, F8, F9, F10, FC1, FC2, FC3, FC4, FC5, FC6, FT9, FT10, C1, C2, C3, C4, C5, C6, T3/T7, T4/T6, CP1, CP2, CP3, CP4, CP5, CP6, TP7, TP8, P1, P2, P3, P4, P5, P6, P7, P8/T8, PO1, PO2, PO3, PO4, PO9, PO10, O1, O2, M1, M2, Lo1, Lo2, Io1, Io2*), embedded in an Electro-Cap (Electro-Cap International, Eaton, OH) or attached to the skin via adhesive patches recorded the EEG. The EEG was recorded at 500 Hz (gain 1000, 16 bit A/D conversion, amplified with a bandpass of .02 – 150Hz). Four electrodes (one below and one near the outer canthus of each eye) recorded vertical and horizontal electrooculogram (EOG) activity. Recordings were referenced to Cz; for analysis, recordings were re-referenced to an average reference (Picton et al., 2000). The EMSE Software Suite (Source Signaling Imaging, San Diego, CA) was used to average ERPs. An algorithm modeling blink and artifact free EEG topography was used to correct blink related artifacts. Sampling epochs were extracted offline and included 300 ms of prestimulus baseline activity and 1200 ms of post-stimulus activity for encoding trials and 300 ms of prestimulus baseline activity and 1500 ms of post-stimulus activity for retrieval trials. The length of the epochs for both encoding and retrieval were chosen because the effects of interest occur within the first 1000 ms of stimulus processing. In addition, participants were instructed to withhold their responses until prompted, and both epoch latencies ended before this prompt. Thus, the EEG should not reflect significant response-related neural activity.

When considering the duration of the prestimulus baseline, it is important to consider that the stimuli (to which the ERPs were time-locked) in Experiments 1 and 2 were preceded by a 100 ms mask. The mask disrupts what would ideally be a relatively

calm and flat segment of the EEG. The integrity of the baseline is important for interpreting potential differences between two waveforms at later segments of the epoch. A prestimulus baseline of 300 ms was chosen so that 200 ms of pre-mask activity could contribute to the prestimulus baseline of the ERP.

Experiment 1 Results

Behavioral Results

Participants' ability to identify the line drawings during the perceptual identification task (at encoding) was quantified as the mean proportion identified. Participants' ability to discriminate between old and new pictures was quantified as the unequal-variance signal detection model discrimination index d_a . Conditional mean d_a values are shown in Figure 11.

Picture identification at encoding. As expected, participants identified nearly all pictures ($M = 0.96$, $SD = 0.04$) in the long encoding condition and nearly half of the all pictures ($M = 0.44$, $SD = 0.15$) in the short encoding condition; the picture identification rate differed reliably between the long and short encoding condition ($t(31) = 21.22$, $SE = .02$, $p < .001$).

Recognition memory. An Encoding Condition (3: long identified, short identified, short unidentified) by Cue Type (2: matching, mirror reversed) ANOVA performed on mean d_a values yielded a main effect of encoding ($F(2, 62) = 361.08$, $MS_E = .45$, $p < .001$, $\eta_p^2 = .92$), which was not accompanied by a main effect of cue type ($F(1, 31) = 2.68$, $p = .11$) or an encoding condition by cue type interaction ($F(2, 62) = 1.18$, $p = .31$). Pairwise comparisons revealed that the main effect of encoding condition reflected the fact that recognition memory in the long identified condition was superior to that of the short identified ($M_{diff} = 1.38$, $SE = .13$, $p < .001$) and unidentified encoding

conditions ($M_{diff} = 3.16$, $SE = .12$, $p < .001$), and recognition memory in the short identified condition was superior to recognition memory in the short unidentified condition ($M_{diff} = 1.78$, $SE = .10$, $p < .001$).

Follow-up tests revealed that recognition memory differed between matching and mirror reversed pictures for short identified pictures ($F(1, 31) = 7.90$, $p < .01$, $\eta_p^2 = .20$); no reliable differences between matching and mirror reversed pictures were present in the other conditions ($F_s < 1.0$). This pattern was substantiated by an encoding by cue type interaction when short identified pictures were separately contrasted with short unidentified pictures ($F(1, 31) = 4.26$, $MS_E = .09$, $p < .05$, $\eta_p^2 = .12$); no such interaction was present however when short identified pictures were contrasted with long identified pictures ($F < 1.0$).

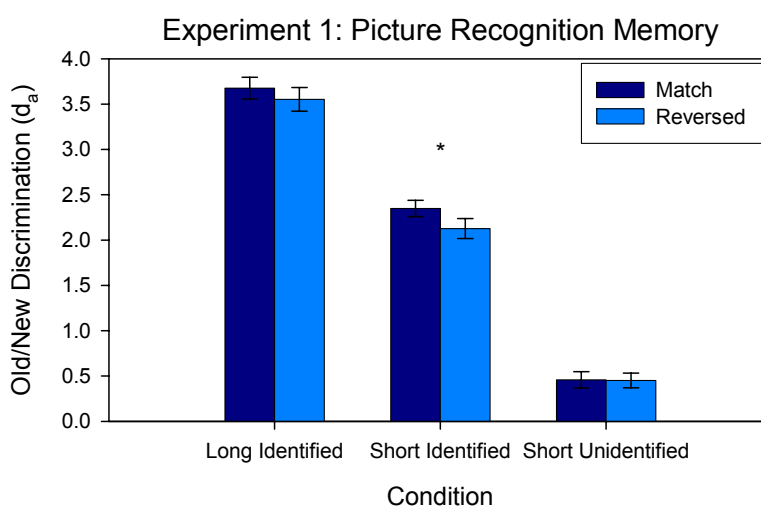


Figure 11. Error bars represent standard error. * denotes a statistically reliable difference in mean recognition memory between matching and mirror reversed pictures.

As can be seen in Figure 11, recognition memory for unidentified matching ($M = 0.46$ $SD = 0.52$) and mirror reversed ($M = 0.45$ $SD = 0.45$) pictures was very low relative to identified pictures. However, these d_a values were numerically similar to previously

reported d_a values for unidentified pictures ($M = 0.43$; Langley & Cleary, 2008), and were reliably above zero (chance memory performance), $t(31)'s > 5.0$, $ps < .001$.

These results are consistent with a number of behavioral studies showing effects of perceptual mismatching on pictures likely recognized on the basis of recollection and familiarity together (e.g., Gardiner et al., 2001, 2005), but not on pictures likely recognized on the basis of familiarity alone (e.g., Verfaellie et al., 2003). Further consideration of these data and their implications are withheld until the Discussion and the General Discussion.

Electrophysiological Results: Waveform Analysis

Differences in subsequent memory. The following data were subjected to a Condition (3: Identified Hit, Unidentified Hit, Unidentified Miss) by Region (4: Anterior Frontal, Frontal, Central, Parietal), by Time (6) by Electrode ANOVA. Smaller, more focused follow-up ANOVAs and paired contrasts were conducted when appropriate. Based on the results of previous research (e.g., Doniger et al., 2000; Schendan & Maher, 2009), specific lateral electrode pairs during specific 100 ms intervals were assessed: (1) 200-300, 300-400, and 400-500 ms for the anterior frontal P250, N350, and N450 at Fp1/Fp2 and AF3/AF4, and N250 and P350 at P7/P8 and PO9/PO10; (2) 300-400, 400-500, and 500-600 for the mid-frontal N350, N390 at F1/F2 and FC1/FC2, and P450 at P7/P8 and PO9/PO10; (3) 500-600, 600-700, and 700-800 for the LPC (*late positive complex*) at C1/C2 and CP1/CP2.

Table 1 provides the F-ratios and η_p^2 -values for the simple effects of condition over each of the four scalp regions and across each of the six time intervals. In Figure 12 ERPs are shown for subsequently recognized identified and unidentified pictures (hits). Only unidentified unrecognized pictures (misses) are shown because accuracy

on the memory test was so high for identified pictures that there were too few identified miss trials.

Over the anterior frontal region of the scalp, identified hits consistently differed from misses for each 100 ms interval between 200-600 ms, and again between 700-800 ms at the Fp1/Fp2 electrode pair, whereas unidentified hits consistently differed from misses between 200-600 ms, and again between 700-800 ms for the at the AF3/AF4 electrode pair; identified hits also differed from misses between 300-400 ms and 400-500 ms at this electrode pair (Figure 12). Identified and unidentified hits did not differ from each other at any time over the anterior frontal scalp.

Table 1.
Simple Effects of Condition (Identified Hits x Unidentified Hits x Misses) by Region and Time

Region	Identification Effects on Subsequent Memory (2, 27)					
	200-300	300-400	400-500	500-600	600-700	700-800
Ant. Frontal						
Fp1/Fp2	\perp 3.26 ^x , .19	\perp 6.73 ^{**} , .33	\perp 6.16 ^{**} , .31	\perp 3.35 ^x , .20	-	\perp 5.60 ^{**} , .29
AF3/AF4	\dagger 4.14 [*] , .23	\dagger 7.63 ^{**} , .36	\dagger 10.20 ^{**} , .43	\dagger 5.32 [*] , .28	-	\dagger 3.28 ^x , .20
Frontal						
F1/F2	-	\dagger 11.70 ^{***} , .46	\dagger 13.25 ^{***} , .50	-	-	-
FC1/FC2	-	\perp 14.52 ^{***} , .52	\dagger 13.98 ^{***} , .50	\perp 4.52 [*] , .25	-	-
Central						
C1/C2	-	\perp 10.43 ^{***} , .44	\dagger 17.83 ^{***} , .57	\dagger 11.46 ^{***} , .46	\perp 3.75 [*] , .22	-
CP1/CP2	-	-	\dagger 6.22 ^{**} , .32	\dagger 12.71 ^{***} , .49	\dagger 4.08 [*] , .23	-
Parietal						
P7/P8	\dagger 31.86 ^{***} , .70	\equiv 46.05 ^{***} , .77	\equiv 38.21 ^{***} , .74	\dagger 33.71 ^{***} , .71	\dagger 8.42 ^{**} , .38	\dagger 9.27 ^{**} , .41
PO9/PO10	\dagger 33.17 ^{***} , .71	\equiv 61.66 ^{***} , .82	\equiv 45.33 ^{***} , .77	\dagger 22.47 ^{***} , .63	\dagger 10.86 ^{***} , .45	\dagger 12.36 ^{***} , .48

Table 1. Simple effects of condition (identified hits, unidentified hits, and unidentified misses) by region and time interval. Each cell shows the F -ratios and η_p^2 . The symbols following the f -values indicate statistical significance of the f -test: - ($p > .07$), ^x ($.07 \leq p \leq .05$), * ($p < .05$), ** ($p < .01$), *** ($p < .001$). The symbols preceding the F -values specify the reliable differences between conditions, as determined by planned pairwise comparisons: \perp (identified hits vs. misses), \dagger (unidentified hits vs. misses), \dagger (unidentified hits vs. misses), \equiv (identified hits vs. unidentified hits, vs. misses).

The N250/Ncl or P250 (200-300 ms). Between 200-300 ms at occipitoparietal (PO09/PO10) electrodes, the mean voltage for misses was less negative than the mean voltage for either identified or unidentified hits, $M_{diff} = 2.45$, $SE = .30$, $p < .001$, $M_{diff} = 1.53$, $SE = .41$, $p < .01$, respectively. Furthermore, identified and unidentified hits did not differ from each other, $M_{diff} = -0.93$, $SE = .43$, $p = .12$. This trend was the same for parietotemporal electrodes (P7/P8). The negative deflection of the ERPs between 200-300 for identified and unidentified hits is the N_{CL} , which has been shown to coincide with the closure of an object's structure, allowing for later processes to determine object identity. The fact that the N_{CL} did not differ for identified and unidentified hits suggests that perceptual closure occurred to a similar extent for both hit types (see Figure 12).

The P350 or N350 (300-500). Over the frontal region of the scalp (F1/F2), the ERPs to unidentified misses were more negative going than the ERPs for both identified and unidentified hits between 300-500 ms, and over the fronto-central scalp region (FC1/FC2) the ERPs to unidentified hits were more negative going than ERPs to identified hits between 400-500 ms (Figure 12), suggesting a graded pattern across trial type. This graded pattern was more apparent over the occipitoparietal region of the scalp between 300-500 ms (see Figure 12, electrodes PO9/PO10), where the effect reversed polarity. Here, the mean voltage for subsequent misses was more positive than the mean voltages for subsequently identified hits *and* subsequently unidentified hits, $M_{diff} = 3.79$, $SE = .34$, $p < .001$, $M_{diff} = 2.00$, $SE = .41$, $p < .001$, respectively. Additionally, unidentified hits were more positive than identified hits, $M_{diff} = 1.79$, $SE = .45$, $p < .001$. As can be seen in Figure 12, this graded pattern was also present between 400-500 ms: misses > unidentified > identified (Table 1); misses vs. unidentified, $M_{diff} = 2.30$, $SE = .36$, $p < .001$; misses vs. identified, $M_{diff} = 4.25$, $SE = .47$,

$p < .001$; unidentified vs. identified, $M_{diff} = 1.95$, $SE = .45$, $p < .001$. This graded pattern suggests that object model selection, as indexed by the N350, occurred to different degrees across condition. Successful object model selection occurred for identified hits, less successful selection occurred for unidentified hits, and object model selection likely failed for unidentified misses.

Figure 12. Experiment 1: Differences in Subsequent Memory

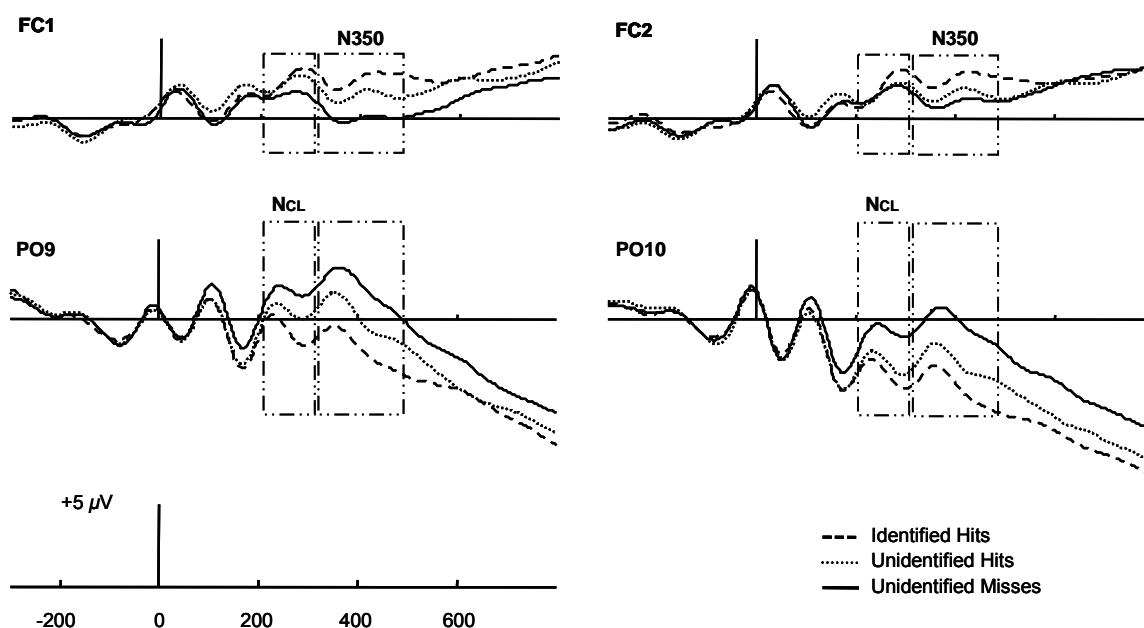


Figure 12. Stimulus-locked grand average ERPs recorded during encoding at fronto-central (FC1/FC2) and parieto-occipital electrodes (PO9/PO10) in Experiment 1. Time scaling ranges from -300 to 800 ms. The latency of the N_{CL} is shaded in dark-gray and the latency of the N350 is shaded in light-gray. Positive deflections are plotted upward. See Appendix A for full electrode figure.

The P350 or N350 (300-500). Over the frontal region of the scalp (F1/F2), the ERPs to unidentified misses were more negative going than the ERPs for both identified and unidentified hits between 300-500 ms, and over the fronto-central scalp region (FC1/FC2) the ERPs to unidentified hits were more negative going than ERPs to identified hits between 400-500 ms (Figure 12), suggesting a graded pattern across trial type. This graded pattern was more apparent over the occipitoparietal region of the scalp between 300-500 ms (see Figure 12, electrodes PO9/PO10), where the effect reversed polarity. Here, the mean voltage for subsequent misses was more positive than the mean voltages for subsequently identified hits *and* subsequently unidentified hits, $M_{diff} = 3.79$, $SE = .34$, $p < .001$, $M_{diff} = 2.00$, $SE = .41$, $p < .001$, respectively.

Additionally, unidentified hits were more positive than identified hits, $M_{diff} = 1.79$, $SE = .45$, $p < .001$. As can be seen in Figure 12, this graded pattern was also present between 400-500 ms: misses > unidentified > identified (Table 1); misses vs. unidentified, $M_{diff} = 2.30$, $SE = .36$, $p < .001$; misses vs. identified, $M_{diff} = 4.25$, $SE = .47$, $p < .001$; unidentified vs. identified, $M_{diff} = 1.95$, $SE = .45$, $p < .001$. This graded pattern suggests that object model selection, as indexed by the N350, occurred to different degrees across condition. Successful object model selection occurred for identified hits, less successful selection occurred for unidentified hits, and object model selection likely failed for unidentified misses.

Electrophysiological Results: Topographic Dissimilarity Analysis

The waveform analyses above imply quantitative differences between conditions, which speak to the relative engagement of a particular population of neurons. However, it is also useful to conduct topographic analyses, which can reveal qualitative differences between conditions. In the absence of quantitative differences, qualitative

differences (differences in the distribution of the electric field at the scalp) imply that distinct brain networks are active for each condition. To examine topographic differences between conditions, the configurational differences between the electric fields for two conditions of interest (conditions are compared in pairs) were assessed by calculating their global dissimilarity (DISS; Lehmann & Skrandies, 1980). DISS is calculated by first normalizing the potentials by dividing each electrode by the instantaneous global field power (GFP)³. DISS is then equal to the square root of the mean squared differences of the GFP-normalized potentials (Murray, Brunet, & Michael, 2008). To determine when the DISS values indicated statistical differences between topographies, an empirical distribution of possible DISS values was generated from individual participant data, which were then compared to the group-averaged DISS values for each time point across the recording epoch. Millisecond-by-millisecond, Figure 13 shows the probability of the empirical distribution having a greater DISS value than that of the group-averaged data, indicating *when* differences between topographies exist.

The topographic dissimilarity analyses show that between identified hits and misses (Figure 13a), reliable topographic differences began at ~184 ms and lasted until the end of the recording epoch (1200 ms). In comparing unidentified hits and misses (Figure 13b), differences were initially present for 90 ms from 84-174 ms. Topographic differences were also present between 242-318 ms and 332-922 ms. Between identified hits and unidentified hits (Figure 13c), short-lived topographic differences were present early, between 68-84 ms. Differences also emerged later, between 358-520 ms, and again between 1044-1142 ms.

³ GFP is the standard deviation across the entire electrode montage at a given moment in time. GFP is used as a reference-

Between 242-318 ms both types of hits differed topographically from misses with no evidence of topographic differences between the two hit types. This is consistent with the known latency of the N250/Nc1 (200-300 ms) and corresponds with the pattern of differences found in the waveform analysis. Between 358-520 ms the three conditions exhibited unique topographic patterns. This corresponds temporally to the graded pattern seen across ERPs at parietal electrode sites, and with the latency of the N350. Given that each topographic difference corresponds to a differences in mean voltage, it is possible that the topographic differences reflect different levels of engagement of the same neural generators as opposed to the activation of distinct neural generators.

independent indicator of a potential's strength, on average, across all electrodes (Lehmann & Skrandies, 1980).

Figure 13. Topographic Differences between Subsequent Memory Conditions

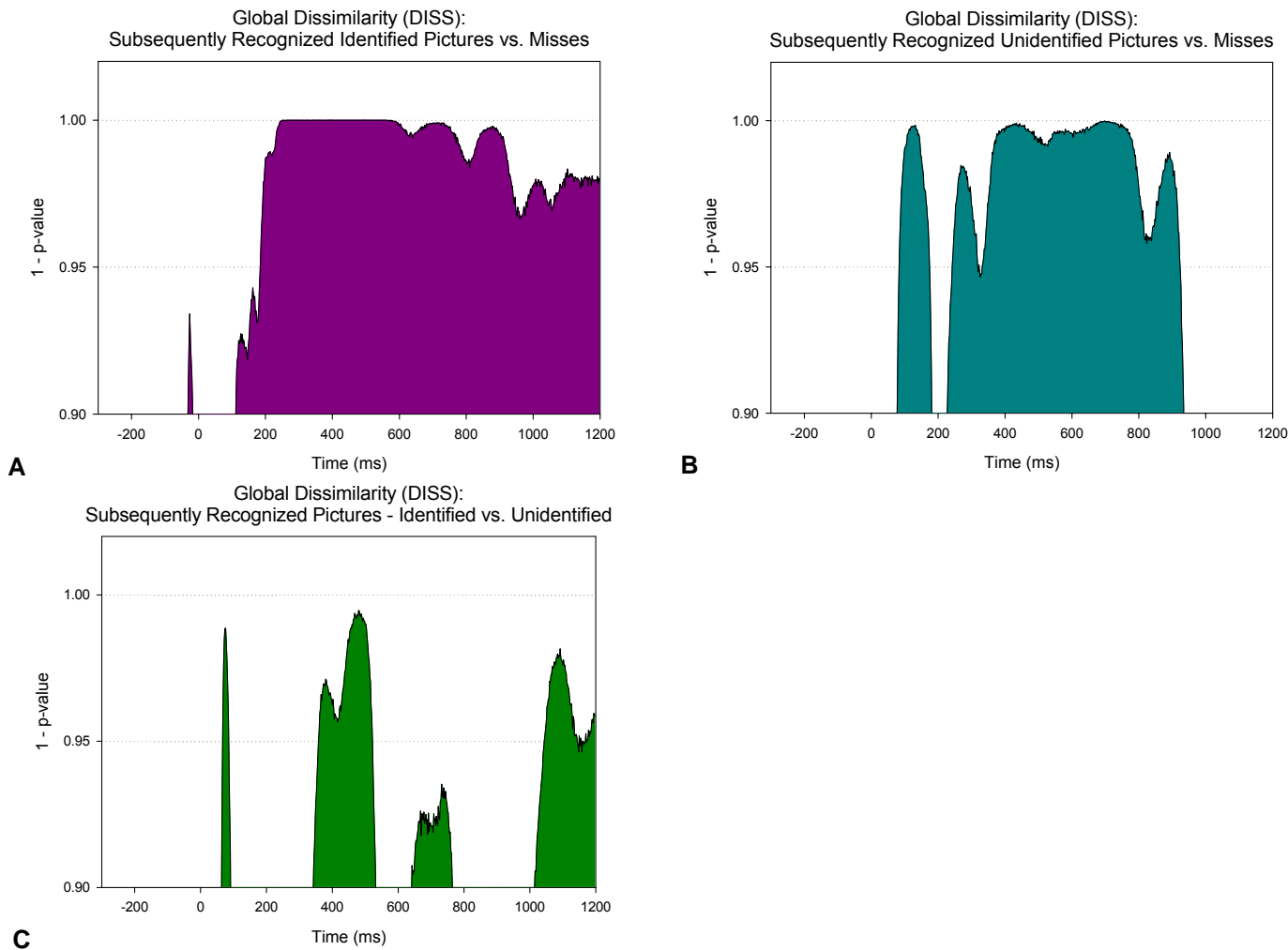


Figure 13. Topographic dissimilarity analysis of ERPs recorded during the encoding phase of Experiment 1. On the y-axis, 1 minus p-values greater than 0.95 indicate statistically reliable differences between the ERP scalp topographies of the conditions being compared. Panel A compares identified hits vs. misses, Panel B compares unidentified hits vs. misses, and Panel C compares hit types.

Retrieval: Old/New Effects

In testing for the presence of old/new effects, the mean voltage of the ERPs elicited by hits were compared to the mean voltage of ERPs elicited by correct rejections from the long encoding condition, resulting in three condition-based contrasts: Identified hits in the long encoding condition vs. correct rejections (long identified condition), identified hits in the short encoding condition vs. correct rejections (short identified condition), and unidentified hits in the short encoding condition vs. correct rejections (unidentified condition). Because the means of the three hit conditions were all compared to the same correct rejection mean, it was not possible to perform a single ANOVAs to compare old/new differences amongst each other. Therefore, separate Time (6) by Condition (2: hit, correct rejection) by Electrode (4) ANOVAs were conducted for each hit type and scalp region. To compare the magnitude of the old/new effects reported below, hits were subjected to a series Region (3) by Condition (2) by Electrode (4) ANOVAs performed separately for each of the six 100 ms intervals. The results of these ANOVAs are provided in Table 2.

Anterior frontal region. Old/new differences over the anterior frontal scalp were detected only for long and short identified picture trials (Table 2). For long identified picture trials, an old/new difference was present between 500-600 ms, although the ERP for old pictures was more negative-going than the ERP waveform for new pictures (the opposite of the pattern typically characterizing explicit recognition memory, see Figure 15, electrodes Fp1/Fp2). It is likely that this old/new difference is a polarity inverted parietal old/new effect that, as will be described below, was present for long identified trails during this time interval. Nevertheless, the mean amplitudes of each of the three hit types did not differ reliably between 500-600 ms (right panel, Figure 14).

Thus, although a reliable reversed-polarity old/new effect was observed for identified long trials, the effect itself was not robust enough to differ from the statistically unreliable differences observed for the other two conditions.

In the short identified condition, an old/new effect was present between 400-500 ms (middle column, Table 2), and was characterized by the typical pattern of a more negative going waveform for new pictures relative to old pictures. As shown in the left panel of Figure 14, mean voltage of differed among hit types between 400-500 ms (right most column, Table 2), with follow-up contrasts confirming that the mean voltage for short identified hits was greater than mean voltage for long identified hits ($F(1, 31) = 12.72, p < .001, \eta_p^2 = .29$). Neither of the two identified hit types differed from unidentified hits.

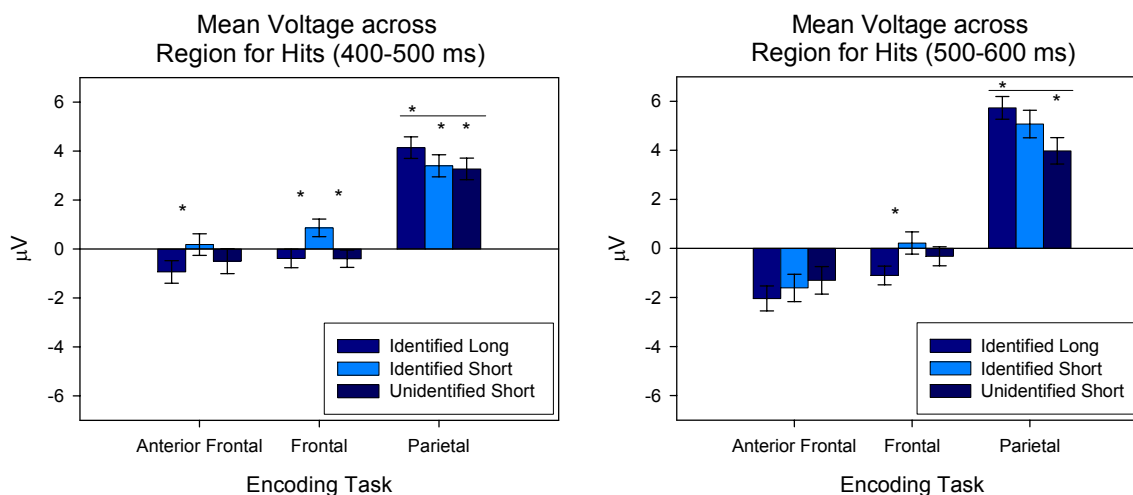


Figure 14. Mean voltage for each hit type across region of the scalp between 400-500 ms (left panel) and between 500-600 ms (right panel). Error bars represent standard error. * indicates a statistically reliable difference between adjacent bars ($p < .05$). An “*” above a horizontal line indicates that the corresponding mean is reliably greater than means corresponding to an “*” below a horizontal line.

Frontal region. Over the frontal scalp, FN400s were present between 300-600 ms. Reliable FN400s were present between 300-500 ms for the long identified condition, between 300-600 ms for the short identified condition, and between 400-600

ms for the unidentified condition; all FN400s were characterized as more negative-going waveforms for new pictures than for old pictures.

Table 2.
F-table for the Simple Effects of Condition across Time and Region

Region	Hits vs. Correct Rejections			Hits
	Long Identified (LI)	Short Identified (SI)	Unidentified (U)	LI x SI x U (2, 30)
200-300 ms				
Ant. Frontal (AF) (1, 31)	-	-	-	-
Frontal (F) (1, 31)	-	-	-	-
Parietal (P) (1, 31)	-	-	-	-
300-400 ms				
Ant. Frontal (AF) (1, 31)	-	-	-	-
Frontal (F) (1, 31)	†12.36**, .29	†27.16***, .47	-	5.13*, .26
Parietal (P) (1, 31)	†5.59*, .15	-	-	-
400-500 ms				
Ant. Frontal (AF) (1, 31)	-	†6.09*, .16	-	6.16**, .29
Frontal (F) (1, 31)	†12.89**, .29	†58.68***, .65	†5.95*, .16	12.03***, .45
Parietal (P) (1, 31)	†9.73**, .24	-	-	8.91**, .37
500-600 ms				
Ant. Frontal (AF) (1, 31)	5.16*, .14	-	-	-
Frontal (F) (1, 31)	-	†23.50***, .43	†4.72*, .13	6.91**, .32
Parietal (P) (1, 31)	†21.93***, .41	†8.52**, .22	-	5.06*, .25
600-700 ms				
Ant. Frontal (AF) (1, 31)	-	-	-	-
Frontal (F) (1, 31)	-	-	-	-
Parietal (P) (1, 31)	-	-	-	-
700-800 ms				
Ant. Frontal (AF) (1, 31)	-	-	-	-
Frontal (F) (1, 31)	-	†4.80*, .13	-	-
Parietal (P) (1, 31)	-	-	-	-

Table 2. The three middle columns report the F -ratios and η_p^2 (partial-eta squared) for the simple effects of condition. The simple effects were the product of a series of Time (6) x Condition (2: hit vs. correct rejection) x Electrode (4) ANOVAs that contrasted mean voltage for hits versus correct rejections separately for each of the three scalp regions (anterior [ant.] frontal, frontal, parietal). The symbol preceding the F -ratios indicates old>new (†). The right-most column reports the F -ratios and η_p^2 for the simple effects of condition resulting from a series of Condition (3: long identified hits, short identified hits, short unidentified hits) x Region (3) x Electrode (4) ANOVAs that contrasted mean voltage for the three hit types separately for each of the six 100 ms intervals. For all four columns, the symbols following the F -ratios indicate statistical significance of the F -test: - ($p > .07$), x ($.07 \leq p < .05$), * ($p < .05$), ** ($p < .01$), *** ($p < .001$).

Mean amplitude for hits varied across condition for each 100 ms interval between 300-600 ms (right-most column of Table 2). Between 300-400 ms, the mean voltage of short identified hits was more positive than that of long identified hits ($F(1, 31) = 8.22, p < .01, \eta_p^2 = .21$) and unidentified hits ($F(1, 31) = 7.48, p < .01, \eta_p^2 = .19$). Shown in Figure 14, the mean voltage of short identified hits was also more positive than the mean voltage for both long identified ($F(1, 31) = 22.53, p < .001, \eta_p^2 = .42$) and for unidentified hits ($F(1, 31) = 13.85, p < .001, \eta_p^2 = .31$) between 400-500 ms, possibly suggesting a stronger familiarity signal for short identified hits. Again, long identified hits and unidentified hits did not differ. Lastly, between 500-600 ms, short identified hits were more positive than and long identified hits ($F(1, 31) = 13.34, p < .001, \eta_p^2 = .30$). No other differences were detected.

Parietal region. As was the case for the FN400, parietal old/new effects were present between 300-600 ms (Table 2). Statistically reliable parietal effects were present for each 100 ms interval between 300-600 ms for the long identified condition, and exclusively between 500-600 ms for the short identified condition; no reliable parietal old/new effects were detected in the unidentified condition. Although the long identified condition was the only condition to produce a reliable old/new effect between 300-400 ms, a one-way ANOVA failed to detect differences in amplitude between long identified hits and hits from the other two conditions, reducing the interpretability of this early difference. The presence of a parietal old/new effect for both types of identified hits, but not unidentified hits, is consistent with the predictions outlined earlier in this chapter that identified pictures would be recognized on the basis of both recollection and familiarity, whereas unidentified pictures would be recognized on the basis of familiarity alone.

Amplitude differences between hit types emerged between 400-500 ms and were reliable until ~600 ms (see right-most column of Table 2). Follow-up contrasts showed that mean amplitude for ERPs to long identified hits was greater than the ERP amplitudes for both short identified hits ($F(1, 31) = 9.34, p < .01, \eta_p^2 = .23$) and unidentified hits ($F(1, 31) = 7.52, p < .01, \eta_p^2 = .20$); amplitude did not differ between short identified and unidentified hits between 400-500 ms.

Figure 15. Retrieval Old/New Effects

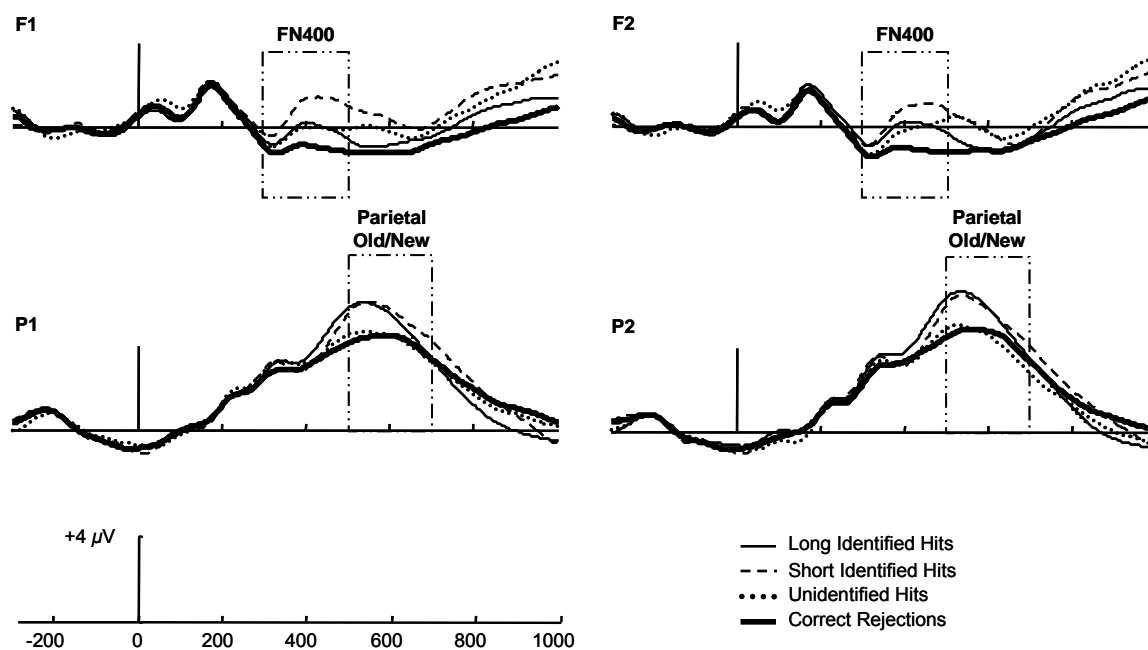


Figure 15. Stimulus-locked grand average ERPs recorded during retrieval at frontal (F1/F2) and parietal electrodes (P1/P2) in Experiment 1. Time scaling ranges from -300 to 1000 ms. The latency of the FN400 is shaded in dark-gray and the latency of the parietal old/new effect is shaded in light-gray. Positive deflections are plotted upward. See Appendix A for full electrode figure.

Between 500-600 ms, however, the amplitudes of ERPs to short and long identified hits were statistically equivalent, suggesting equivalent degrees of recollection. While the amplitude of the ERP to long identified hits was greater than that of

unidentified hits ($F(1, 31) = 9.90, p < .01, \eta_p^2 = .24$), ERP amplitudes for identified short hits and unidentified hits did not differ.

Topographic Analysis of Retrieval ERPs

Topographic Dissimilarity Analysis. Results of the topographic dissimilarity analyses (Figure 16) illustrates that distinct scalp topographies existed between each of the three hit types and correct rejections (henceforth referred to as topographic old/new effects). Topographic old/new effects were present from 290–690 ms and 746–1000 ms for short identified pictures (Figure 16a), from 332-542 ms and 762-1000 ms for long identified pictures (Figure 16c), and from 400–1000 ms for unidentified pictures (Figure 16e). For each of the three conditions, the topographic old/new effects roughly correspond to the ERP old/new differences that were identified in the waveform analysis (primarily between 400-500 ms). This suggests that both quantitative and qualitative differences in neural activity for recognized and unrecognized novel pictures existed during latencies known to correspond to successful retrieval of episodic memory.

To determine how the topographic old/new effects, themselves, differed between conditions, three dissimilarity analyses were conducted on old-new differences waves (hits – correct rejections): long identified vs. short identified (Figure 16b), short identified vs. unidentified (Figure 16d), and long identified vs. unidentified (Figure 16f). As can be seen in the right column of Figure 16, between 200-800 ms, topographic old/new effects between short identified and long identified pictures differed during two distinct intervals: 458-538, 664-740 ms (Figure 16b). Topographic old/new effects also differed between two distinct intervals for long identified and unidentified pictures between 278-420 ms and 478-584 ms (Figure 16d), and for topographic old new differences between short identified and unidentified pictures differed between 300-330 ms and 534-642 ms

(Figure 16f).

These patterns are largely consistent with what one would expect on the basis of the waveform analysis. For example, an FN400 was present for both short identified hits and short unidentified hits between 400-500 ms, and no difference between the topographic old/new effects were present during this interval for short identified and unidentified pictures (Figure 16f). This suggests that no qualitative differences existed between the old/new effects for short identified and unidentified pictures. Likewise, a parietal old/new effect was present for short identified pictures but not unidentified pictures between 500-600 ms. Consistent with this pattern, differences were present for the topographic old/new effect contrast of short identified and unidentified pictures (Figure 16f). This pattern was expected given that old/new differences were present for short identified pictures over the parietal region of the scalp, were not present over the parietal scalp for unidentified pictures. In general, this pattern is consistent with the notion that a distinct recollection process was engaged for identified hits that was *not* also engaged for unidentified hits.

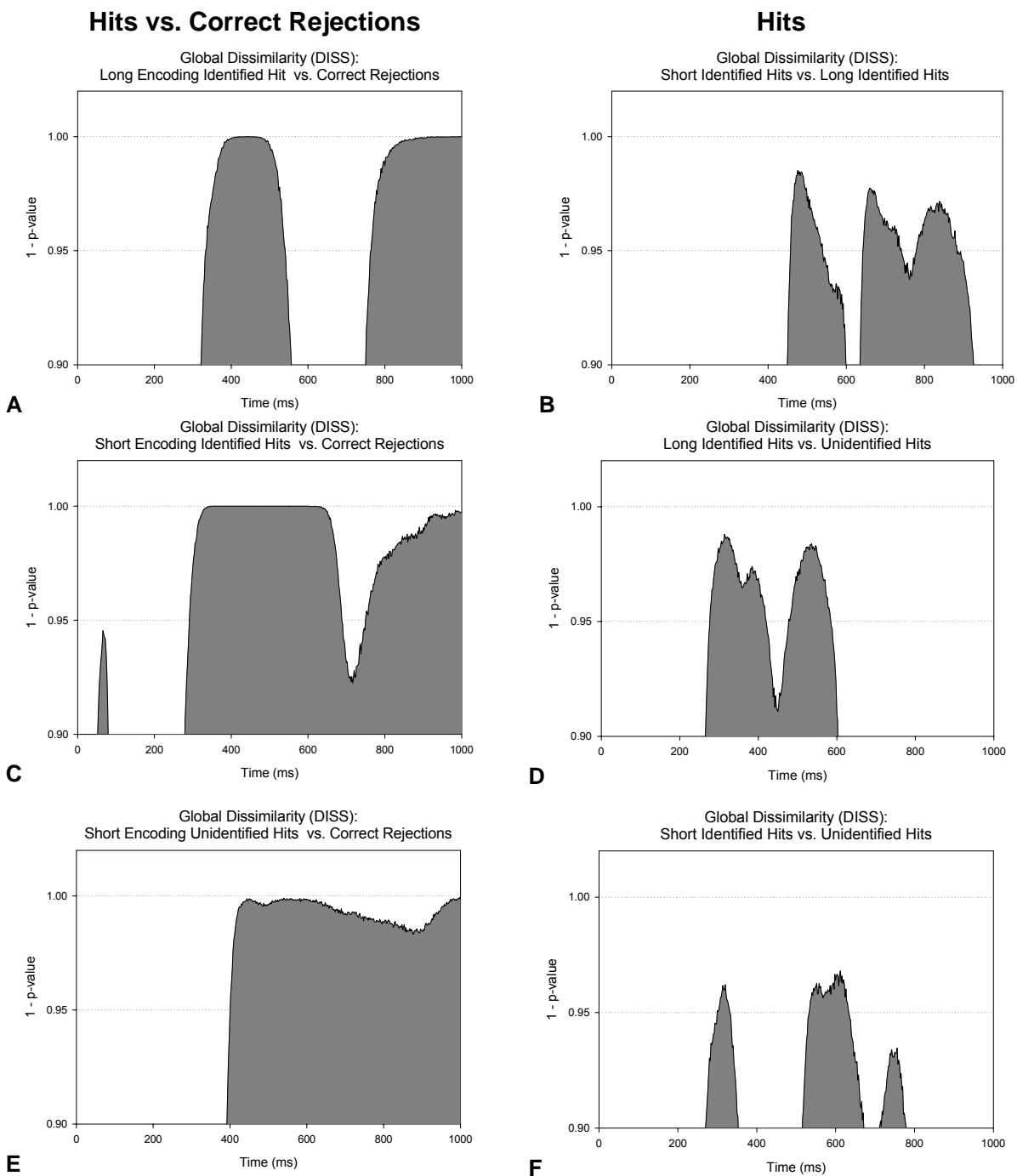
Figure 16. Global Topographic Dissimilarity between Hits and Correct Rejections

Figure 16. Topographic dissimilarity analysis of ERPs recorded during the retrieval phase of Experiment 1. On the y-axis, 1 minus p-values greater than 0.95 indicate statistically reliable differences between the ERP scalp topographies of the conditions being compared. Panels A, C, and E compare hits with correct rejections, whereas Panels B, D, and F compare hit types.

Discussion of Experiment 1 Results

The goals of Experiment 1 were two-fold. The first goal was to determine whether the putative neural correlate of familiarity (FN400) would be present for recognized pictures that were not identified by name during encoding (RWPI effect), and if so, whether the FN400 would be present in the absence of the putative neural correlate of recollection (parietal old/new effect) for these trials. It was predicted that recognition memory for identified pictures in both encoding conditions would be based on both recollection and familiarity, and would therefore elicit an FN400 and a parietal old/new effect. The behavioral data replicated previous studies by demonstrating a RWPI effect for briefly presented, masked pictures, so, as implied above, it also was predicted that recognition memory for unidentified pictures would be familiarity-based, and consequently would elicit only an FN400.

The retrieval data showed that between 400-500 ms, an FN400 was present for recognized pictures not identified during encoding. Moreover, no parietal old/new effect was observed at any point during the retrieval epoch for unidentified pictures. The data for unidentified pictures that were later recognized stand in contrast to the data for recognized pictures that were identified either during the long or short encoding tasks. For such pictures, both an FN400 and a parietal old/new effect were observed. The FN400 was present between 300-500 ms for identified pictures in the long encoding condition, and between 400-600 ms for pictures in the short encoding condition. When the FN400 was present for identified pictures in the long encoding condition *and* unidentified pictures, their effects were consistently of lesser amplitudes than the effect for identified pictures in the short encoding condition, with the exception of the 500-600 ms interval where identified and unidentified pictures in the short encoding condition did

not appear to differ. The FN400 was present in all three conditions only during the 400-500 ms interval.

Clear parietal effects were found in the long identified condition between 400-600 ms, whereas for the short identified condition the parietal effect was present only between 500-600 ms. No parietal effect was present for unidentified pictures. Thus, the main finding within the retrieval data was that an FN400, in the absence of a parietal old/new effect, was present only for recognized pictures that were not identified at encoding. These data suggest that when impoverished encoding conditions prevent a picture from being identified by name, subsequent recognition of the picture is likely based on familiarity.

The second goal of Experiment 1 was to examine the sequence of neural activity that unfolded during the perceptual identification task (encoding task). The purpose was to identify the earliest separation between ERPs for subsequently recognized identified and unidentified pictures. The running assumption was that the timing of this separation would point to the last stage of unimpeded object processing undergone by the unidentified pictures, and that this would provide insight into the type of features that might have been stored in the pictorial memory trace. It was predicted that subsequently recognized unidentified pictures would undergo perceptual closure (N_{CL}), but not object model selection/object categorization (N350). This prediction was based on the results of previous research (Bacon-Mace, Mace, Fabre-Thorpe, & Thorp, 2005) that has suggested that the backward masking during encoding disrupts categorization of a picture, and that such disruption would be seen as a modulation of the N350 (Shendan & Kutas, 2007).

A difference was observed during the 200-300 ms interval between subsequent

misses and both subsequent hit types, suggests that subsequently missed pictures did not achieve the same degree of closure (if at all) as identified and unidentified pictures that were subsequently recognized. In addition, ERPs to unidentified hits did not differ from ERPs to identified hits between 200-300 ms over the parietal region of the scalp, suggesting that perceptual closure was achieved to a similar extent for both types of subsequently recognized pictures.

Assuming that the N350/P350 indexes a search of the perceptual representations system, the graded pattern seen over the parietal region of the scalp between 300-500 ms suggests that participants recovered non-diagnostic information during the encoding of unidentified pictures that were subsequently forgotten, resulting in a large N350. The N350 for unidentified subsequent hits was smaller in amplitude than it was for unidentified misses, suggesting that participants recovered more object information on unidentified hit trials. The N350 for identified hits was the smallest in amplitude, which is consistent with predictions from the literature. That is, the attenuation of the N350 for identified hits implies that both complete object component recovery and model selection occurred and, therefore, a less extensive search of the structural description system was undertaken on these trials. The fact that the N350 was larger for unidentified hits than for identified hits implies that a more extensive search of the structural description system occurred for unidentified hit trials, possibly because the object components that were recovered yielded matches to many structural object descriptions (Schendan & Kutas, 2007). The ERP data do not definitively indicate whether or not the search of the structural description system was successful for unidentified hit trials. However, successful matching of a perceptually closed object representation to a structural description allows for object categorization to occur, which

presumably would have been followed by conscious object naming. Obviously, the status of these trials as “unidentified” indicates that object naming did not occur. Based on the present data, therefore it seems most plausible to infer that object model selection did not occur.

After accepting the inferences that subsequently recognized unidentified pictures were perceptually closed, and that structural description representations were activated for these pictures in the absence of successful object model selection, the implications for the potential contents of the pictorial memory trace are more straightforward. Given that the structural description system representations houses representations that are visually abstract (Cooper, Schacter, Ballesteros, & Moore, 1994; Kourtzi & Kanwisher, 2001; Schendan & Kutas, 2007), attributes such as picture identity episodic context, local features, and other perceptual specifics housed in the episodic representation system (e.g., orientation, size) are unlikely candidates for components of the pictorial memory trace for picture not identified at encoding. Thus, with regard to perceptual information, it would seem that abstract visual information in the form of global object structure or the general configuration of an object’s component parts (possibly *geons*, Biederman, 1987) are the most plausible candidates. With regard to other forms of information, it is very possible that conceptual/semantic information is also stored with the pictorial memory trace for unidentified masked pictures. As pointed out by Schendan and Kutas (2007), the N350 reflects a neural system that supports perceptual *and* conceptual implicit memory, “generic memory” (Hintzman, 1978), in addition to object model selection. The data from the present experiment, however, cannot speak to this issue as conceptual processing was not directly manipulated.

Considering the data from retrieval within the context of the data from encoding,

the suggestion is that the successful familiarity-based recognition of pictures that were not identified at encoding in Experiment 1 may have been based on non-episodic, abstract perceptual information, and potentially some as-of-yet unspecified conceptual/semantic information. Both possibilities are explored in Experiment 2.

CHAPTER 7: EXPERIMENT 2

A primary goal of Experiment 2 was to expand upon the capacity of the design used in Experiment 1 to shed light on the type information capable of supporting familiarity-based recognition. This goal was approached in the following ways: First, previous research has demonstrated the potential of inclusion/exclusion retrieval instructions to alter the relevancy of a stimulus' perceptual versus conceptual attributes during a recognition memory test (e.g., ; Stenberg et al., 2006). With regard to familiarity specifically, Ecker and Zimmer (2009) found that the FN400 was sensitive to study-test congruency, but that it depended on the retrieval instructions.

In Ecker and Zimmer's (2009) study, they presented participants with pictures during encoding, and with either new pictures, old pictures, or exemplar old pictures (same object, different instance; see Figure 17) during test trials. In one condition participants were instructed during the memory test to endorse both identical studied pictures and different exemplars of studied pictures as old (inclusion instructions). In the second condition, participants were instructed during the memory test to only endorse identical studied pictures as old (exclusion instructions). Ecker and Zimmer argued that reducing the relevance of the stimuli's perceptual attributes during a memory test by introducing *inclusion* instructions should bias participants toward evaluating test pictures on a more conceptual level (Ecker & Zimmer, 2009; Stenberg et al., 2006). The logic was that the matching of perceptual features between encoding and retrieval would not be relevant to whether participants endorse the test pictures as old or new, as exemplar pictures would not match perceptually but were still to be endorsed as old. Consistent with this idea, Ecker and Zimmer found an FN400 for both types of test pictures in the inclusion condition, with the effect being larger for identical pictures than for exemplar

pictures.

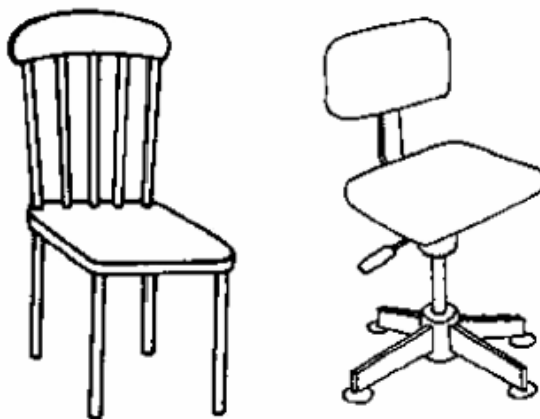


Figure 17. Example of exemplar stimuli (same/different).

Under *exclusion* retrieval instruction conditions, the stimuli's perceptual attributes would be particularly relevant (Stenberg et al., 2006), as only test pictures that were perceptually identical to those shown at encoding were to be endorsed as old. In fact, relying on conceptual matches between encoding and retrieval would lead to the incorrect endorsement of exemplars under exclusion instructions, as decisions based on conceptual information alone would not be able to distinguish between identical and exemplar pictures (conceptually identical). For the inclusion condition, Ecker and Zimmer observed an FN400 only for identical pictures, a finding that was consistent with the logic of using the exclusion instructions. They interpreted the whole of their findings as evidence that familiarity is not just data-driven, but also influenced by top-down processes (retrieval orientation).

The authors rightly point out that familiarity is quite often described as an “undifferentiated feeling of prior occurrence” (see Rugg & Curran, 2007), but argue that

this does not preclude the influence of an objects conceptual and perceptual features in the production of the “undifferentiated” memory signal. Ecker and Zimmer further argue that the role of such perceptual and conceptual information plays in familiarity-based memory likely depends on task demands (or task-dependent strategies)—a idea that challenges the widely held view that familiarity is a highly automatic, and by extension an inflexible, process (e.g., Yonelinas, 2002). If true, the manipulation of participants’ retrieval orientation could provide a means of further specifying the type of information that supported the recognition of unidentified pictures in Experiment 1.

Manipulating retrieval orientation within the context of the RWPI procedure should bias participants’ processing of the test stimuli toward perceptual or conceptual attributes, depending on the retrieval instructions. If the memory trace for unidentified pictures contain primarily abstract perceptual representations, as could possibly be inferred from the results of Experiment 1, one might expect exclusion instructions to improve memory performance because participants would be biased toward processing the type of stimulus attributes (perceptual) that are dominate in the picture’s memory trace, thereby making more salient the match between what is being perceived and what is stored in memory. Conversely, if an substantial degree of conceptual information was part of the memory trace for unidentified pictures (which cannot be ruled out on the basis of the results of Experiment 1), one might expect equivalent memory between retrieval instruction conditions, or possibly superior memory following inclusion instructions. In either case, the outcome would be informative about the nature of what is stored in the memory trace for unidentified pictures, and the types of information that are capable of serving as evidence for familiarity judgments.

There is reason to suspect that manipulations at encoding may also be

informative about the type of information contained within the pictorial memory trace for pictures unidentified during encoding. Recall that the ERP encoding data from Experiment 1 suggest convincingly that the critical difference between unidentified pictures that were subsequently remembered and unidentified pictures that were subsequently forgotten was the success of the perceptual closure process. Moreover, a difference was also apparent between these trials for the N350, which, as already described, is a component thought to reflect a search of perceptual representations. Thus, it stands to reason that additional resources devoted to perceptual processing at encoding may further facilitate the formation of memory traces for unidentified pictures that are accessed during retrieval. Likewise, it is plausible that increased attention to conceptual components of the stimuli could bolster the memory trace by increasing the proportion of conceptual pictorial information.

With regard to the effects of encoding task on the neural correlates of retrieval, anticipating the outcome is more difficult. One reason for this is because ERP studies that have intentionally manipulated encoding task have not done so in a way that orients participants towards attending to either perceptual attributes of to-be-remembered stimuli or conceptual/semantic attributes to-be-remembered stimuli. Rather, the dichotomy is typically in terms of “shallow” and “deep” processing (Craik & Lockhart, 1972). The majority of “deep” encoding instructions do involve participants processing the stimuli on a meaningful level (e.g., is the object depicted living or non-living, Duarte et al., 2004; Otten & Rugg, 2001). However, the majority of “shallow” processing instructions do not specifically orient participants towards stimuli’s perceptual attributes. Rather, such instructions orient participants towards processing the stimuli in ways that generally that avoid meaningful processing. Examples of such superficial processing

instructions include instructing participants to determine (a) whether the first and last letter of a name/word are in alphabetical order (Otten & Rugg, 2001; Rugg et al., 2000) or whether the word's vowels are in alphabetic order (Allan et al., 2002) or the number of syllables in the word (Fay, Isingrini, Ragot, & Pouthas, 2005), (b) whether the object is manipulable (Duarte et al. 2004; Otten & Rugg, 2001), and (c) whether the object is left or right of a fixation point (Iidaka, Matsumoto, Nogawa, Yamamoto, & Sadato, 2006). Thus, there is little past research on which to base predictions about perceptual and conceptual encoding manipulations in ERP research.

A second reason that the results of a perceptual/conceptual encoding task manipulation are difficult to anticipate is because the results of ERP studies that have examined more general encoding task manipulations on retrieval have produced conflicting results. That is, some studies report little to no modulation of familiarity related old/new effects (e.g., Rugg et al., 1998) while others report considerable modulation of familiarity old/new effects (e.g., Rugg et al., 2000). Moreover, some studies imply that stimulus class (Allan et al., 2000) or intent to remember (van Hooff, 2005) have more pronounced effects on ERPs at retrieval. In these latter cases, the general finding is only that waveforms will be more positive for the condition that should produce better memory (e.g., more memorable stimulus classes, like pictures relative to words, and intentional versus incidental encoding instructions, respectively).

In Experiment 2 an inclusion/exclusion manipulation was added to the retrieval phase of the current design in order to assess the claims of Ecker and Zimmer (2009). In addition, an encoding instruction manipulation was added to the encoding phase of Experiment 2, despite the ambiguity that exists regarding its effectiveness. The encoding manipulation required that participants attend to the conceptual attributes of

the pictures (a living/non-living judgment) or the visual/physical attributes of the stimulus (a judgment regarding the lines contained within the picture). To the degree that this manipulation may direct processing to different attributes of the of the study-list stimuli, it creates the appropriate experimental conditions for the emergence of dissociations between conceptual and perceptual processes at encoding and retrieval.

Method

Participants

Thirty Iowa State University undergraduates (mean age: 20.2 years, range: 18-28, 7 females) participated in exchange for research participation credit in a lower-level psychology course. All participants provided informed consent, and the study was approved by the Human Participant Institutional Review Board of Iowa State University. Participants were randomly assigned to one of two retrieval instruction conditions, the inclusion condition ($n = 15$) or the exclusion condition ($n = 15$).

Materials and Design

Two sets of 512 line drawings were used in the present experiment. For clarity, I refer to the two picture sets as Picture Set A and Picture Set B. Set A is composed of images that are exemplars of the images in Set B. That is, for every object or animal (e.g., pencil, gorilla) depicted by an image in Set A, a different instance (i.e., exemplar) of the same object or animal is depicted in Set B. Images corresponding in this way between the two sets share the same name and categorical identity, but the visual characteristics of the two images are distinct (see Figure 17).

Each picture set was divided in half, resulting if four sets of 256 pictures. One of these halves (256 pictures) from Sets A and B were assigned to serve as “old” stimuli and the remaining pictures served as “new” stimuli. Across four study-test blocks, a

given participant would study a total of 256 pictures from *either* Set A or Set B. During memory testing, half of all “old” pictures (128 pictures) were from Set A and half were from Set B. In other words, half of the old test pictures were exact perceptual matches to pictures presented during encoding and the other half were exemplar pictures. Likewise, half of all new stimuli presented at test were from Set A and the other half were from Set B. Assignment of Old/New status to pictures from Sets A and B was counterbalanced across participants.

Procedure

Participants were randomly assigned to either the inclusion condition or the exclusion condition. Before the onset of the experiment, participants were run through a short practice session that familiarized them with the encoding and retrieval sequences. The initial instructions in the practice session explained to participants that the experiment would involve the brief presentation of masked picture, and that they would be asked to judge whether the pictures was of a living or non-living object (animacy encoding), or whether the picture was composed of more horizontal lines or more vertical lines (line encoding). To respond to question about the picture, participants pressed the “v” key (living, or horizontal) or the “b” key (non-living, vertical). After making either the animacy or the line decision, participants were to name the picture aloud. During the practice session, participants perceptually identified four pictures in the line encoding task, and four pictures in the animacy encoding task (in separate blocks).

In the next phase of the practice session, the instructions indicated that participants would receive a memory test for the pictures they had just seen.

Participants were presented with one of two instructional displays (Appendix B), which

explained that some of the pictures on the test would be identical to those shown in the encoding phase, while others would be a different instance (exemplar) of a seen picture. Participants in the inclusion condition were instructed to endorse a picture as old, even if the picture had changed in its visual form (top panel of Appendix B); participants in the exclusion instruction condition were instructed to endorse pictures as old only if they were identical to what was seen previously (bottom panel of Appendix B). Participants were then shown an instructional display that described how their memory response should be made. The display (Appendix C) instructed participants that in making their old/new discriminations, they should indicate yes (the picture was studied) or no (the picture is new) on a 6-point scale (Yes:1 2 3 | 4 5 6 :No). Responses of “1” indicated a high certainty in their yes response, and “6” a high certainty in their no response (see Appendix C). Numbers toward the middle of the scale (e.g., 3, 4) indicated the lowest certainty in their responses. Responses 1-6 on the rating scale corresponded to keys X-M on the bottom row of the keyboard (see Appendix C). Participants then engaged in four test trials on which they practiced making their memory response.

In both conditions, participants completed two study-test blocks. Within each block, participants attempted to perceptually identify 128 masked pictures (the timing for the fixation, mask, and stimulus *presentation sequence* was identical to that used in the short encoding condition of Experiment 1; see Figure 10). However, prior to each fixation, participants were presented with one of two cues (“living/non-living,” or “horizontal/vertical”; assignment of encoding task to block was counterbalanced across participant). The cues appeared for 1000 ms, and were followed by a blank screen for 1000 ms before the onset of the fixation cross (1000 ms). The forward and backward masked picture was presented immediately after the fixation cross offset (see Figure

10).

Following the picture's presentation, participants were asked to provide their living/non-living horizontal/vertical judgment (like during the practice trials). After making their response, participants were prompted to identify the picture aloud. Half of all encoding trials were accompanied by the living/non-living (animacy) task and the other half were accompanied by the horizontal/vertical (line) task.

At test, participants discriminated between 64 perceptually matching studied pictures, 64 conceptually matching exemplar pictures, and 128 pictures that were both perceptually and conceptually novel. Following their yes-no rating, participants were asked to provide a source memory judgment about the test picture. When asked "*What decision did you make for this picture?*", participants chose from the following options: 2 = "*Horizontal/Vertical Lines,*" 3 = "*Living/Non-Living,*" 3 = "*I don't know,*" and 4 = "*It was new.*"

Electrophysiological recording and analysis. The electrophysiological recording and statistical analysis in the present experiment were identical to that of Experiment 1 unless stated otherwise. That is, the same array of 68 scalp electrodes, recording parameters (e.g., digitized at 500 Hz, etc.), and analysis software and artifact correction algorithms were used in Experiment 2 that were used in Experiment 1.

Experiment 2 Results

Behavioral Results and Discussion

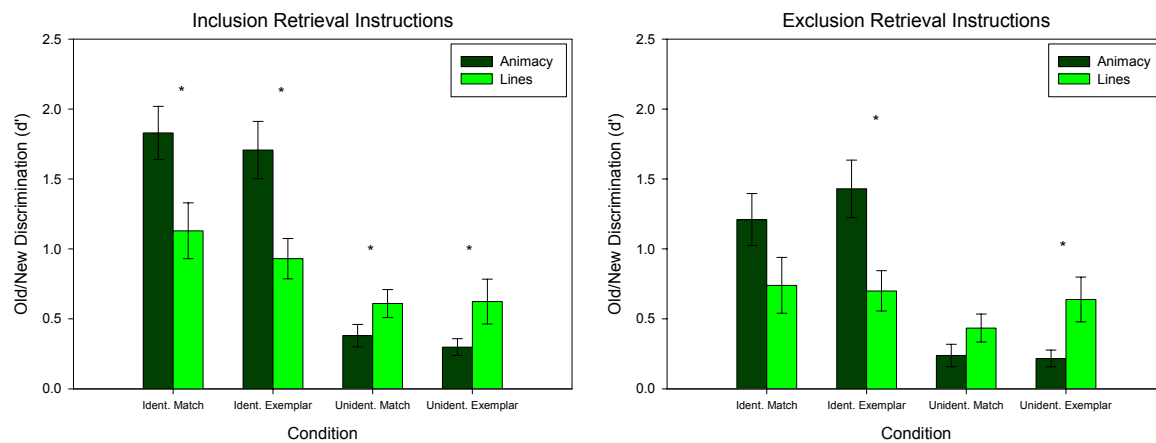
As in Experiment 1, participants' ability to identify line drawings during the perceptual identification task (at encoding) was quantified as the mean proportion identified. Participants' ability to discriminate between old and new pictures was quantified as the UVSD model discrimination index d_a . Conditional mean d_a values are

shown in Figure 18.

Picture identification at encoding. Participants' identification rates were approximately 30% in both the inclusion condition ($M = 30.55$, $SD = 0.15$) and the exclusion condition ($M = 30.01$, $SD = 0.14$), with no reliable differences detected between groups ($t < 1.0$).

Recognition memory. Although participants' old/new discrimination was relatively low for unidentified pictures (d 's < 0.7) relative to identified pictures (d 's ≥ 0.7), discrimination was significantly above chance ($d' = 0$) for all unidentified picture conditions (p s $< .05$; see Figure 18). Thus, the behavioral results of Experiment replicate and extend the findings of Experiment 1 and of previous studies by showing that RWPI occurs when (a) participants are asked to make judgments about the stimuli in addition to the task of identifying the stimulus by name, and (b) when exclusion instructions are given to participants during retrieval.

To examine the effects of the encoding and retrieval manipulations on picture recognition, a retrieval instruction (2: inclusion vs. exclusion) by encoding task (2: animacy vs. lines) by test cue type (2: matching picture vs. exemplar picture) by identification status (2: identified vs. unidentified) mixed ANOVA was conducted. The ANOVA revealed an encoding by match by identification status interaction, $F(1, 28) = 5.83$, $MS_E = .10$, $p < .05$, $\eta_p^2 = .17$, along with main effects of encoding, $F(1, 28) = 10.11$, $MS_E = .28$, $p < .01$, $\eta_p^2 = .27$, identification status, $F(1, 28) = 142.05$, $MS_E = .36$, $p < .001$, $\eta_p^2 = .80$, and retrieval instruction, $F(1, 28) = 4.25$, $MS_E = .88$, $p < .05$, $\eta_p^2 = .13$.

Figure 18. Experiment 2: Picture Recognition Memory**Figure 18.** Error bars represent standard error. * denotes a statistically reliable difference in mean recognition memory between pictures encoded in the animacy and line tasks.

In follow-up analyses on the three-way interaction, paired comparisons for identified pictures revealed that differences between encoding tasks were present for matching test-pictures that were recognized under inclusion instructions, and exemplar test-pictures recognized under both inclusion and exclusion instructions. In all cases, these differences showed greater memory following animacy encoding than following line encoding ($p_s < .05$). For unidentified pictures, differences between encoding tasks were observed for exemplar test-pictures under both inclusion and exclusion instructions ($p_s < .05$), and for matching test-pictures under inclusion instructions ($p = .05$). After collapsing across variables of retrieval instruction and test cue type, this trend was substantiated by an encoding by identification status cross-over interaction ($F(1, 28) = 20.77, MS_E = .82, p < .001, \eta_p^2 = .43$), with paired contrasts showing that picture recognition was better in the animacy task than in the line task for identified pictures ($F(1, 28) = 17.90, p < .001, \eta_p^2 = .39$), while picture recognition was better in the line task than in the animacy task for unidentified pictures ($F(1, 28) = 15.95, p < .001, \eta_p^2 = .36$).

Follow-up analyses exploring the main effects showed that the main effect of encoding was reliable for both identified pictures ($F(1, 28) = 17.90$, $MS_E = 1.00$, $p < .001$, $\eta_p^2 = .39$) and unidentified pictures ($F(1, 28) = 15.95$, $MS_E = .16$, $p < .001$, $\eta_p^2 = .36$) separately. The main effect of retrieval instruction was reliable for identified pictures ($F(1, 28) = 5.86$, $MS_E = .85$, $p < .05$, $\eta_p^2 = .17$), but not unidentified pictures ($F < 1.0$). This dissociation was substantiated by an identification status by retrieval instruction interaction ($F(1, 28) = 4.00$, $MS_E = .36$, $p = .05$, $\eta_p^2 = .13$). Furthermore, paired comparisons indicated that picture memory differed as a function of retrieval instructions (inclusion > exclusion) only for identified matching pictures that were initially encoded in the animacy task ($p < .05$). No direct differences between matching and exemplar pictures were observed in any condition.

Figure 19. Experiment 2: Picture Source Memory

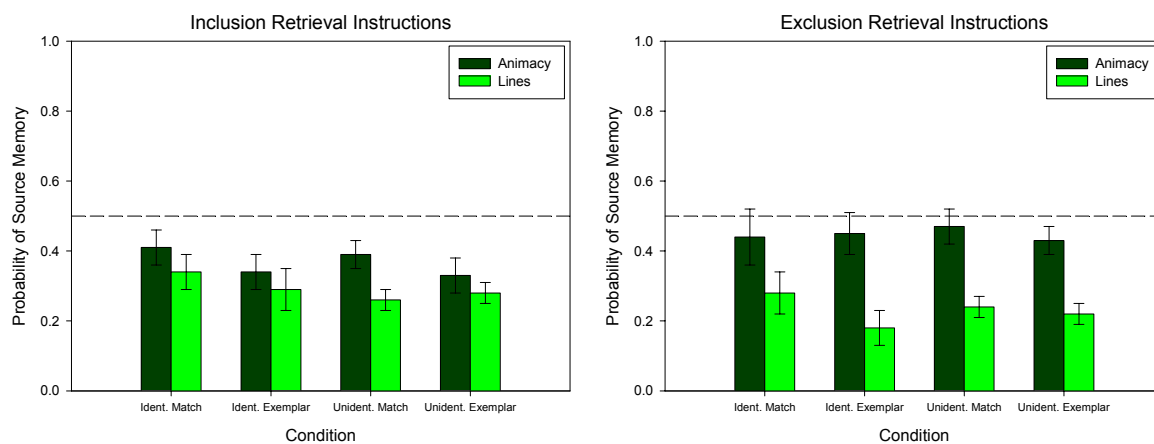


Figure 19. Error bars represent standard error. The dashed line indicates chance performance level.

Source memory. To further characterize recognition memory during retrieval, the accuracy of participants' source memory judgments were examined to assess the degree to which the recall of episodic details may have contributed to picture recognition. As shown in Figure 19, participants accuracy in recalling the context (i.e.,

the encoding task) in which an old test item was studied was at or below chance (0.50) across all conditions. This suggests that the retrieval of certain contextual details present during a given stimulus's encoding did not contribute in a measurable way to picture recognition during retrieval.

Discussion of Behavioral Results

The behavioral recognition memory results of Experiment 2 yielded four main results. First, the data revealed opposite effects of encoding task on recognition memory for identified and unidentified pictures, showing that orienting participants' processing toward perceptual or conceptual processing has different effects on how well identified and unidentified pictures are later recognized. Second, effects of retrieval instruction were limited to recognition of identified pictures following the animacy encoding task. Third, no effects of perceptual mismatching were found for either identified or unidentified pictures. Fourth source memory was at or below chance for both identified and unidentified pictures in all conditions.

The effect of encoding task is of most interest because it demonstrates a dissociation between recognition for identified and unidentified pictures. Many behavioral studies have shown that deeper, semantic levels of processing benefit both recollection and familiarity, with recollection generally benefiting more than familiarity (e.g., Gardiner, 1988; Gregg & Gardiner, 1994; Khoe et al., 2000; Rajaram, 1993; Toth, 1996; Wagner et al., 1997; Yonelinas, 2001). While some studies have shown size congruency effects only on recollection (Gardiner, Ramponi, & Richardson-Klavehn, 1999; Java, Gregg, & Gardiner, 1997), few studies have shown benefits of shallow (or perceptual) encoding on familiarity over deep (or conceptual) processing (Rajaram, 1993).

Nevertheless, the greater RWPI effect for the line encoding condition over the animacy encoding condition is consistent with a prediction described at the outset of this chapter. Specifically, it was suggested that if unidentified pictures at encoding led to memory traces consisting of primarily of perceptual information, and if this perceptual information played a key role in the unidentified picture's later recognition, then orienting participants towards perceptual information during encoding could have improved encoding of this critical perceptual material and led to better recognition during retrieval.

Given the potentially large role of perceptual processing in the RWPI effect observed here (such that it was larger following perceptual encoding relative to conceptual encoding), it may be tempting to attribute the results to perceptual priming. However, it would be difficult to explain the RWPI effects observed in Experiment 2 through a perceptual priming account given the lack of perceptual mismatching effects observed between matching and exemplar pictures. Numerous studies have demonstrated the consistent and reliable decrease of perceptual priming following substantial changes to the perceptual characteristics of a picture or object, such as when exemplars are shown at test (e.g., Bar & Biederman, 2001; Biederman & Cooper, 1991a, 1991b), while familiarity-based recognition has been shown in some cases to be unaffected even when the format of the stimuli has changed (picture vs. word; Langley, 2008; Lebreton, Desgranges, Landaeu, Eustache, & Baron, 2001) or when modality has changed (auditory vs. visual; Rajaram, 1993). Given that there was no decline in recognition memory for exemplar pictures, perceptual priming seems an unlikely explanation. Conceptual priming also seems an unlikely explanation, given that the more conceptually oriented encoding task led to worse recognition memory than did the more perceptually oriented encoding task. Thus, the RWPI effects observed here were

likely explicit in nature.

If the RWPI effects reported here are explicit, largely perceptual in nature, and not affected by changes in visual form (exemplars), a logical assumption is that the perceptual information driving the effect is abstract. The stimuli used for this experiment were not selected in such a way that all exemplars were different in their structural description relative to their counterparts. In fact, many of the pictures in the stimulus set appear to share a similar global shape with their exemplar counterparts. Therefore, it is possible for abstract perceptual representations that are specific only with respect to global structure to support memory for both identical picture repetitions and exemplar pictures. As was the case in Experiment 1, it is not possible to rule out the contribution of conceptual information. However, the fact that a conceptual processing orientation during encoding lead to worse memory than did a perceptual orientation suggests, at the very least, that the contribution of conceptual processing does not dominate over the contribution of perceptual processing.

Electrophysiological Results: Waveform Analysis

Animacy encoding task. The ERP data from encoding were subjected to a Condition (3: Identified Hit, Unidentified Hit, Unidentified Miss) x Region (4: Anterior Frontal, Frontal, Central, Parietal) x Time (6: 200-300, 300-400, 400-500, 500-600, 600-700, 700-800) x Electrode (4) omnibus ANOVA with smaller, more focused, follow-up ANOVAs and pairwise comparisons when appropriate. Table 3 provides F-values and η_p^2 -values of the simple effects of condition over each of the four scalp regions and across each of the six time intervals. Figure 20 shows ERPs for subsequently recognized identified and unidentified pictures (hits) and subsequently forgotten unidentified pictures (misses) for the animacy encoding condition.

The N250/Nc1 or P250 (200-300 ms). Between 200-300 ms, effects of condition were present over the parietooccipital scalp region (see Table 3, second column from left; also see Figure 20). Pairwise comparisons confirmed that mean voltage for both identified and unidentified hits were more negative than for misses during the latency of the N250 ($M_{diff} = 1.69$, $SE = .63$, $p < .05$, $M_{diff} = 1.06$, $SE = .38$, $p < .05$, respectively); mean voltage for identified and unidentified hits did not differ ($M_{diff} = -0.63$, $SE = .45$, $p = .52$), suggesting no quantitative differences in the N250 between the two hit types.

The P350 or N350 (300-500). Between 400-500 ms, effects of condition were observed over the frontal scalp region (see Table 3 and Figure 20), with pairwise comparisons showing that the mean voltage for identified hits was less negative than the mean voltages for both unidentified hits and misses ($M_{diff} = 1.78$, $SE = .53$, $p < .01$, $M_{diff} = 2.24$, $SE = .73$, $p < .05$, respectively). Mean voltage for unidentified hits and misses did not differ ($M_{diff} = 0.45$, $SE = .53$, $p = .90$), suggesting that the N350 was present for both unidentified hits and misses to a similar degree.

Region	Identification Effects on Subsequent Memory (2, 22)					
	200-300	300-400	400-500	500-600	600-700	700-800
Anterior Frontal	-	-	-	-	-	-
Frontal	-	-	$\pm 5.93^*$, .35	-	-	-
Central	-	-	$\ddagger 3.12^x$, .22	$\ddagger 3.40^x$, .24	-	-
Parietal	$\pm 4.11^*$, .27	$\pm 6.00^{**}$, .35	$\pm 7.65^*$, .41	$\pm 4.86^*$, .31	-	-

Table 3. Simple effects of condition (identified hits, unidentified hits, and unidentified misses) by region and time interval. Each cell shows the f-value and partial-eta squared. The symbols following the f-values indicate statistical significance of the f-test: - ($p > .07$), x ($.07 \leq p \leq .05$), * ($p < .05$), ** ($p < .01$), *** ($p < .001$). The symbols preceding the f-values specify the reliable differences between conditions, as determined by planned pairwise comparisons: \pm (identified hits vs. misses), \ddagger (identified hits vs. unidentified hits), † (unidentified hits vs. misses), \equiv (identified hits vs. unidentified hits, vs. misses).

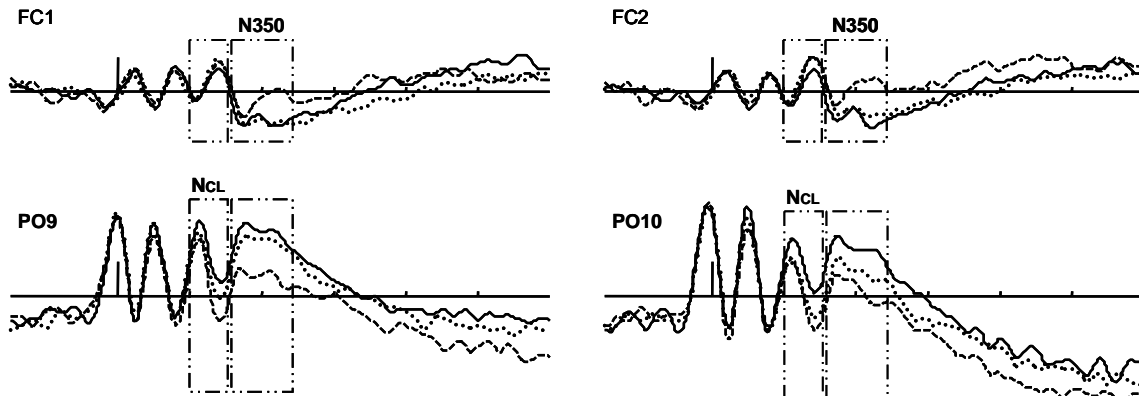
Line encoding task. Figure 20 shows ERPs for subsequently recognized identified and unidentified pictures (hits) and subsequently forgotten unidentified pictures (misses) for the line encoding condition. As can be seen in both Figure 20 and Table 4, no statistically reliable effects of condition were observed between 200-800 ms over any of the four scalp regions. One marginally reliable effect of condition was observed over the parietal scalp between 400-500 ms (see Table 4). This marginal effect of condition was driven by a marginally less positive mean voltage for unidentified hits than misses ($M_{diff} = 0.98$, $SE = .41$, $p = .07$). Identified hits did not differ from unidentified hits or misses (p 's $> .45$). It seems unlikely that this marginal difference reflects an old/new difference that is predictive of subsequent memory, especially given that the difference was not observed between identified hits and misses. Likewise, the difference does not appear to correspond to any of the known object identification ERPs.

Region	Identification Effects on Subsequent Memory (2, 22)					
	200-300	300-400	400-500	500-600	600-700	700-800
Frontal Anterior	-	-	-	-	-	-
Frontal	-	-	-	-	-	-
Central	-	-	-	-	-	-
Parietal	-	-	[†] 2.97 ^x , .21	-	-	-

Table 4. Simple effects of condition (identified hits, unidentified hits, and unidentified misses) by region and time interval. Each cell shows the f-value and partial-eta squared. The symbols following the f-values indicate statistical significance of the f-test: - ($p > .07$), ^x ($.07 \leq p \leq .05$), * ($p < .05$), ** ($p < .01$), *** ($p < .001$). The symbols preceding the f-values specify the reliable differences between conditions, as determined by planned pairwise comparisons: [‡] (identified hits vs. misses), [†] (identified hits vs. unidentified this), [†] (unidentified hits vs. misses), [≡] (identified hits vs. unidentified hits, vs. misses).

Figure 20. Subsequent Memory ERPs for Animacy and Line Encoding Tasks

Animacy Task



Line Task

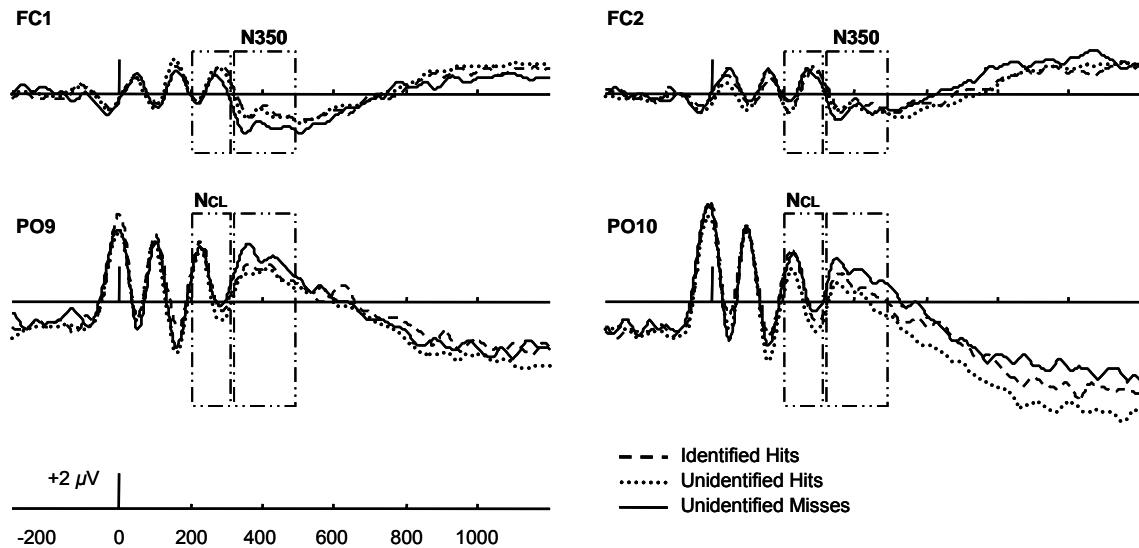


Figure 20. Stimulus-locked grand average ERPs recorded during encoding at fronto-central (FC1/FC2) and parieto-occipital electrodes (PO9/PO10) in Experiment 2. The upper four plots show ERPs from the animacy encoding task, and the lower four plots show ERPs from the line encoding task. Time scaling ranges from -300 to 1200 ms. The latency of the N_{CL} is shaded in dark-gray and the latency of the N_{350} is shaded in light-gray. Positive deflections are plotted upward. See Appendix A for full electrode figure.

Effects of Encoding Task on Encoding ERPs

To examine the effects of the encoding tasks themselves on ERPs recorded during encoding, an initial Task (2) by Condition (3) by Time (6) x Electrode (4) ANOVA was performed for each of the four regions in order to identify the scalp regions over which condition effects were present. Task by condition interactions were observed for the frontal ($F(2, 46) = 3.44, p < .05, \eta_p^2 = .13$) and parietal ($F(2, 46) = 6.50, p < .01, \eta_p^2 = .22$) regions. Neither a main effect of task or condition were present for the frontal region, but both were present for the parietal region ($F(1, 23) = 4.62, p < .05, \eta_p^2 = .17, F(2, 46) = 5.16, p < .01, \eta_p^2 = .18$, respectively).

Given that the reliable task by condition interactions described above were present only over the frontal and parietal regions, more focused ANOVAs were limited to these regions. These ANOVAs were further restricted to comparisons of two conditions, subsequent hit vs. subsequent miss, so that possible differences between remembered and forgotten pictures could be examined. The ANOVAs revealed the presence of Task (2) by Condition (2: identified hits vs. unidentified misses) interactions for both the frontal region ($F(1, 23) = 4.09, p = .05, \eta_p^2 = .15$) and the parietal region ($F(1, 23) = 7.75, p < .05, \eta_p^2 = .25$). No main effects of task were present for either region and there was no main effect of condition for the frontal region ($F_s < 1.0$). There was a reliable main effect of condition for the parietal region ($F(1, 23) = 6.97, p < .05, \eta_p^2 = .23$), however. No 2 x 2 interactions were present when the ANOVAs were performed using unidentified hits in the place of identified hits.

Follow-up Task (2) by Condition (2) by Electrode (4) ANOVAs were conducted separately for each time period for the frontal and parietal regions to better define the task by condition interactions. Task by condition interactions were observed over the

frontal scalp between 400-500 ms ($F(1, 23) = 4.71$ $p < .05$, $\eta_p^2 = .17$) and 700-800 ms ($F(1, 23) = 6.12$ $p < .05$, $\eta_p^2 = .21$), with a marginally reliable main effect of condition ($F(1, 23) = 4.12$ $p = .05$, $\eta_p^2 = .15$) during the 400-500 ms interval. Over the parietal scalp, interactions were present during all six time intervals (all F 's > 5.4 , p 's $< .05$, η_p^2 's $> .20$), with main effects of condition present for each 100 ms time interval between 300-600 ms (F 's > 7.45 , p 's $\leq .01$, η_p^2 's $> .25$). Post-hoc contrasts confirmed that the task by condition interactions between 200-700 ms over the parietal scalp and between 400-500 ms over the frontal scalp were the result of condition differences only within the animacy task (all F 's > 4.20 , p 's $\leq .05$, η_p^2 's $> .16$) and that only misses varied between tasks (misses were more negative over the frontal region of the scalp and more positive over the parietal scalp in the animacy task; all F 's > 4.30 , p 's $< .05$, η_p^2 's $> .16$). This means that the encoding task manipulation selectively affected ERPs to subsequently missed pictures. The differences observed for subsequently missed pictures between tasks likely explains why no reliable effects were observed for ERPs in the line encoding task. Further consideration to this is given in the Discussion.

Electrophysiological Results: Topographic Dissimilarity Analysis.

Consistent with the results of the waveform analysis, the topographic dissimilarity analysis found topographic differences between hits and misses only in the animacy condition (see Figure 21). Specifically, identified animacy hits differed topographically from unidentified animacy misses between 342-382 ms and 420-478 ms (Figure 21a). Unidentified animacy hits also differed from unidentified animacy misses between 236-298 ms, 316-328 ms, and again between 452-460 ms (Figure 21c). The topographic difference between 236-298 ms likely corresponds to the N_{CL} , and coincides with ERP differences observed for the N_{CL} during this interval.

Topographic differences between identified hits and unidentified hits were present between 248-280 ms, and again between 346-548 ms (Figure 21e). The latter difference is consistent with the ERP differences observed between subsequent hit types for the animacy encoding condition between 400-600 ms. Although the former topographic difference did not correspond to any difference observed in the ERP analysis, it did correspond to latency of the N_{CL} . In general, the topographic analyses do not strongly indicate that unique neural generators were active between conditions. Rather, the topographic results support the findings from the waveform analysis in that specific object related processes were engaged to different degrees in different conditions. This point is elaborated on in the Discussion.

Figure 21. Topographic Dissimilarity for Subsequent Memory

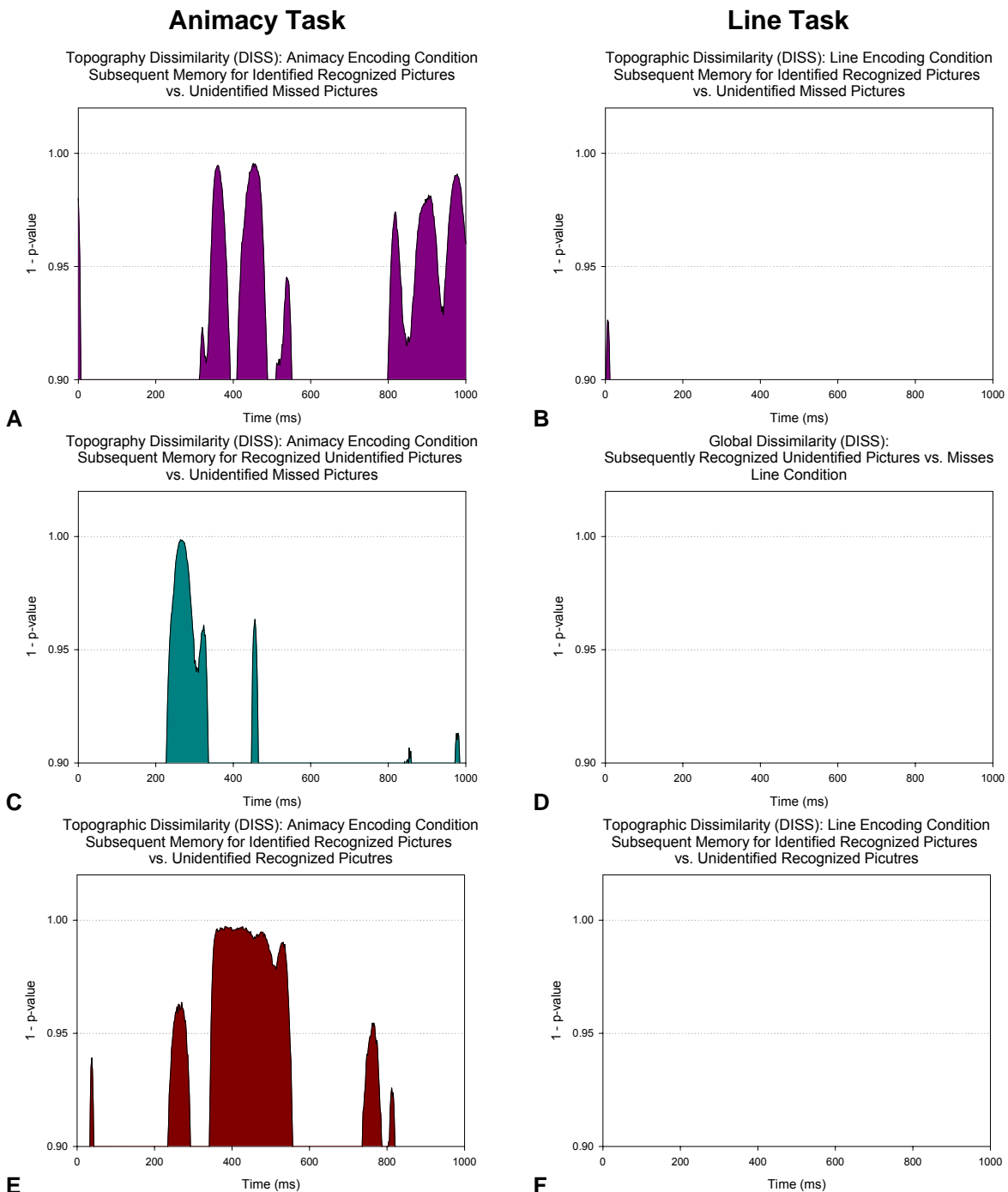


Figure 21. Topographic dissimilarity analysis of ERPs recorded during the encoding phase of Experiment 2. On the y-axis, 1 minus p-values greater than 0.95 indicate statistically reliable differences between the ERP scalp topographies of the conditions being compared. Panels A, C, and E compare animacy task conditions, and Panels B, D, and F compare line task conditions. Note that the empty plots in Panels A, C, and E indicate that there were no topographic differences.

Retrieval: Old/New Differences

As in Experiment 1, separate Time (6) by Condition (2: hit, correct rejection) by Electrode (4) ANOVAs were conducted for each hit type and scalp region. To compare the magnitude of the old/new effects reported below, hits were subjected to a series Region (3) by Condition (2) by Electrode (4) ANOVA performed separately for each of the six 100 ms intervals.

Inclusion Instructions. No differences between ERPs for correct rejections and recognized pictures (hits) encoded in the animacy task and retrieved under inclusion instructions were detected (Figure 22). However, for recognized pictures encoded in the line task (Figure 22) and retrieved under inclusion instructions, reliable differences between ERPs for unidentified matching hits and correct rejections were present over the anterior frontal scalp region between 300-500 ms ($F(1, 10) = 6.50, p < .05, \eta_p^2 = .39$) and over the frontal scalp region between 200-400 ms ($F(1, 10) = 9.32, p < .01, \eta_p^2 = .48$). In both cases, the mean voltage for matching hits was more negative than for correct rejections. Parietal differences were not observed for matching or exemplar pictures. In summary, no differences of interest were found during a test of memory for picture encoded during the animacy task and retrieved under inclusion conditions. When pictures encoded in the line task were retrieved under inclusion conditions, a reversed polarity FN400 was present.

Exclusion Instructions. Under exclusion instructions, ERPs for pictures encoded in the animacy task showed old/new differences over the frontal scalp region for matching pictures ($F(1, 10) = 6.31, p < .05, \eta_p^2 = .39$) and exemplar pictures ($F(1, 10) = 6.31, p < .05, \eta_p^2 = .39$) between 300-400 ms (see upper panels of Figure 23). In both cases, the differences reflected more negative mean voltage for hits.

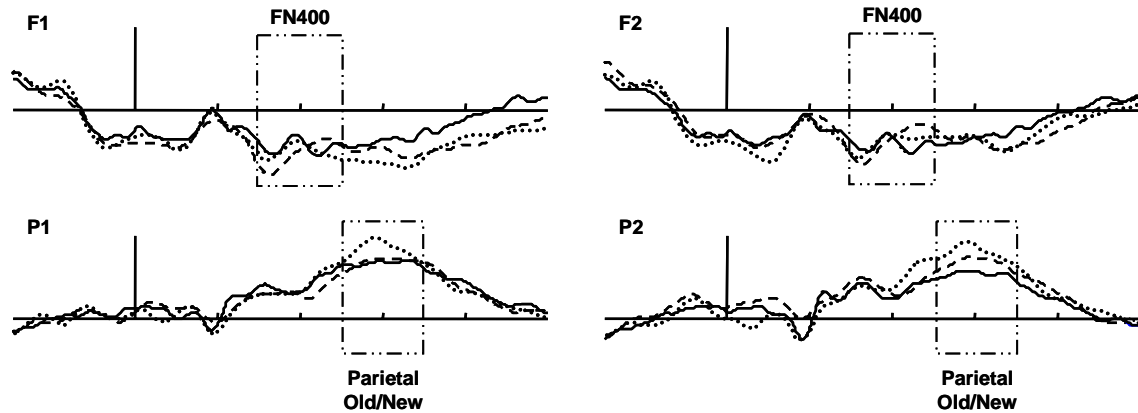
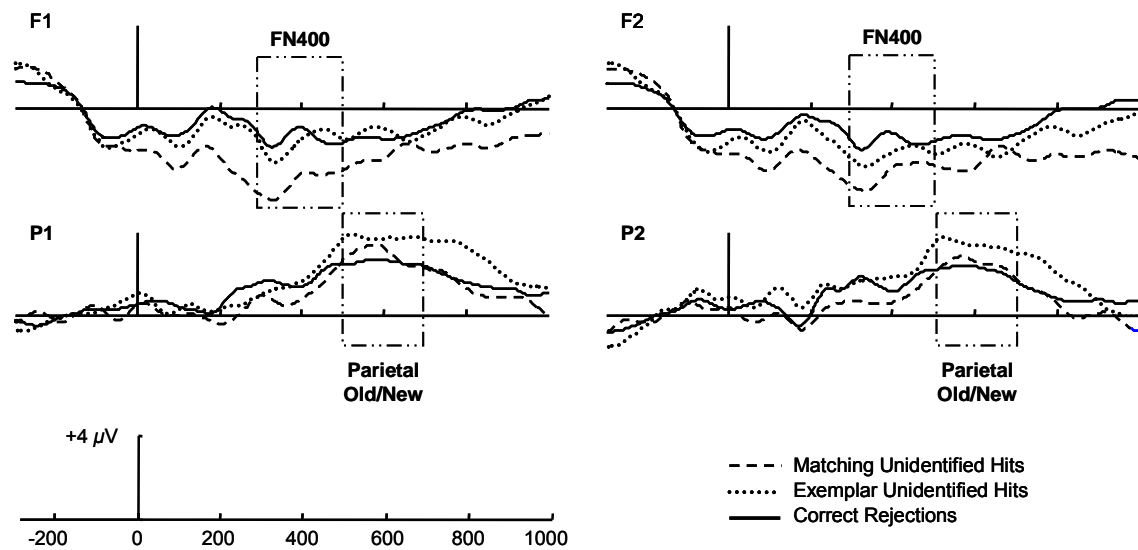
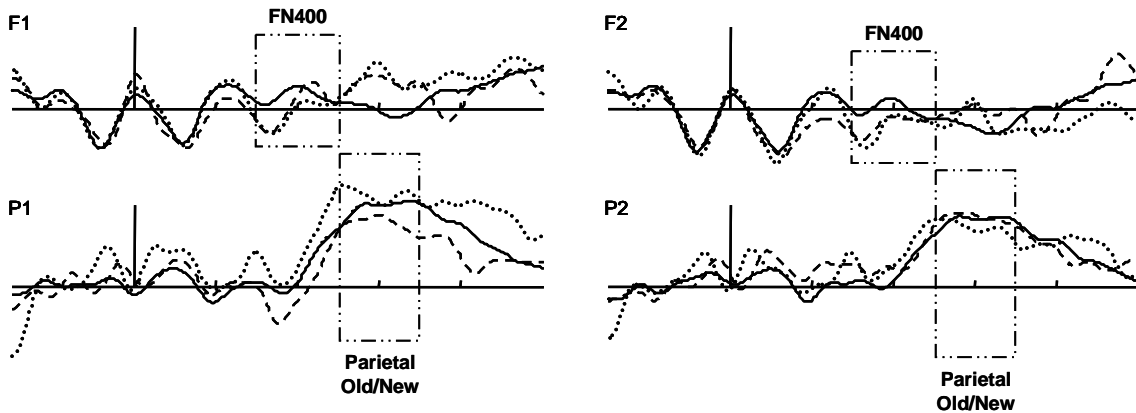
Figure 22. Old/New Recognition ERPs – Inclusion Instructions**Animacy Task****Line Task**

Figure 22. Stimulus-locked grand average ERPs recorded under inclusion retrieval instructions at frontal (F1/F2) and parietal electrodes (P1/P2) in Experiment 2. The upper four plots show ERPs for pictures encoded during the animacy task, and the lower four plots show ERPs for pictures encoded during the line task. Time scaling ranges from -300 to 1000 ms. The latency of the FN400 is shaded in dark-gray and the latency of the parietal old/new effect is shaded in light-gray. Positive deflections are plotted upward. See Appendix A for full electrode figure.

Figure 23. Old/New Recognition ERPs – Exclusion Instructions

Animacy Task



Line Task

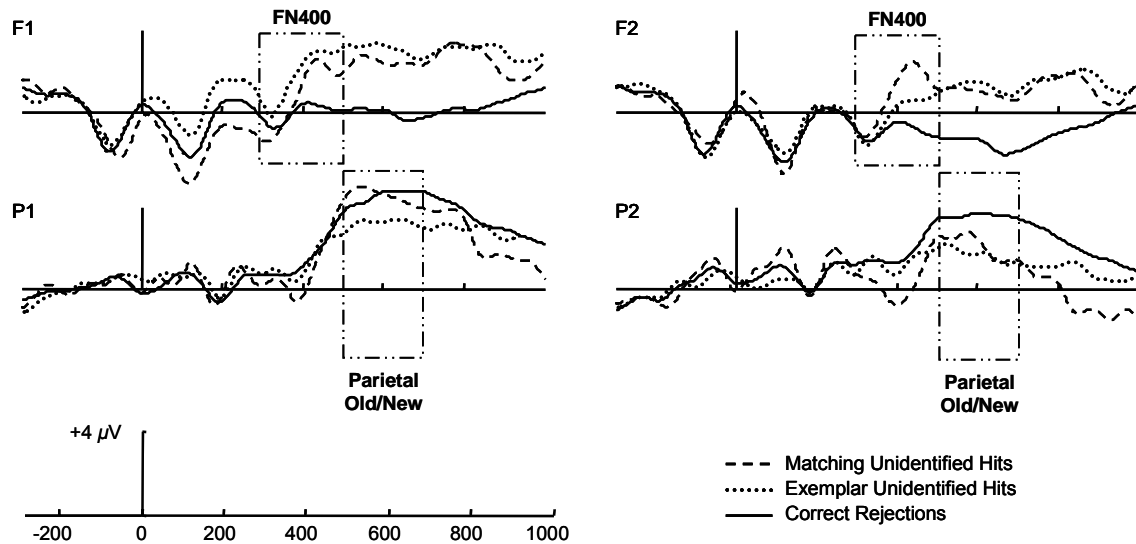


Figure 23. Stimulus-locked grand average ERPs recorded under exclusion retrieval instructions at frontal (F1/F2) and parietal electrodes (P1/P2) in Experiment 2. The upper four plots show ERPs for pictures encoded during the animacy task, and the lower four plots show ERPs for pictures encoded during the line task. Time scaling ranges from -300 to 1000 ms. The latency of the FN400 is shaded in dark-gray and the latency of the parietal old/new effect is shaded in light-gray. Positive deflections are plotted upward. See Appendix A for full electrode figure.

ERPs for pictures encoded in the line task showed old/new differences over the frontal scalp between 400-500 ms ($F(1, 10) = 8.79, p < .05, \eta_p^2 = .47$) and 600-800 ms ($F(1, 10) = 7.90, p < .05, \eta_p^2 = .44$) for matching pictures, and between 500-800 ms ($F(1, 10) = 8.32, p < .05, \eta_p^2 = .45$) for exemplar pictures (lower panels of Figure 23). In all cases, hits were more positive than correct rejections, and therefore constituted an FN400. The mean amplitude of the ERPs for matching and exemplar hits did not differ between 400-800 ms ($F_s < 1.0$), suggesting that the FN400 (between 400-500 ms) was equivalent for both types of test cues.

Effects of Encoding Task and Retrieval Instruction on Old/New Differences

In the previous set of analyses, old/new differences were observed under each of the two types of retrieval instructions and following each of the two encoding tasks. Specifically, old/new differences that were observed under inclusion retrieval instruction conditions were detected only for pictures encoded during the line task, whereas old/new differences that were observed under exclusion retrieval instructions were detected for pictures encoded in either the line or the animacy task. The old/new effects were observed over the anterior frontal and frontal regions of the scalp, occurring between 200-800 ms. With the old/new effects isolated, the following analyses sought to examine how the old/new effects differed as a function of the encoding and retrieval condition manipulations employed in Experiment 2. In doing so, a series of Encoding Task (2: Animacy vs. Lines) by Condition (2: Hit vs. Correct Rejection) by Retrieval Instruction (2: Inclusion vs. Exclusion) by Electrode (4) ANOVAs were performed separately on ERPs recorded over the anterior frontal and frontal scalp regions during each of the six 100 ms intervals.

Anterior frontal scalp. When including matching pictures as the hit type, the 2 x

2 x 2 x 4 ANOVAs revealed only a main effect of retrieval task over the anterior frontal scalp region between 300-400 ms ($F(1, 20) = 6.45$, $MS_E = 136.46$, $p < .05$, $\eta_p^2 = .24$). Pairwise comparisons showed that the main effect was the result of hits for pictures encoded during the line task being more positive under exclusion instructions than under inclusion conditions ($F(1, 20) = 9.10$, $MS_E = 8.96$, $p < .05$, $\eta_p^2 = .31$) and correct rejections following animacy encoding being more positive under exclusion instructions than under inclusion instructions ($F(1, 20) = 8.73$, $MS_E = 8.15$, $p < .05$, $\eta_p^2 = .30$). No main effects or interactions were observed for exemplar pictures.

Frontal scalp. When including matching pictures as the hit type, the 2 x 2 x 2 x 4 ANOVAs revealed encoding task by condition by retrieval instruction interactions over the frontal region of the scalp between 300-400 ms (see Figure 24; $F(1, 20) = 5.66$, $MS_E = 7.93$, $p < .05$, $\eta_p^2 = .22$), 400-500 ms (see Figure 25; $F(1, 20) = 10.85$, $MS_E = 8.96$, $p < .01$, $\eta_p^2 = .35$) and 700-800 ms ($F(1, 20) = 7.01$, $MS_E = 10.06$, $p < .05$, $\eta_p^2 = .26$). For unidentified exemplar hits, a three-way interaction was only observed over the frontal region of the scalp between 400-500 ms (see Figure 25; $F(1, 20) = 4.75$, $MS_E = 7.34$, $p < .05$, $\eta_p^2 = .19$). No main effects or lower-order interactions were present.

For matching pictures, main effects of retrieval instruction accompanied the interactions present during the 300-400 ms and 400-500 ms intervals ($F_s > 5.0$, $p_s < .05$), and a main effect of condition accompanied the interaction present during the 300-400 ms interval ($F(1, 20) = 5.70$, $MS_E = 8.01$, $p < .05$, $\eta_p^2 = .22$). For both the 300-400 ms and 400-500 ms intervals, the main effects of retrieval instruction more negative-going ERPs following inclusion instructions than following exclusion instructions (Figures 25 and 26, respectively). For the 300-400 ms interval, the main effect of condition reflected more negative-going ERPs for matching hits than correct rejections (Figure

24).

Follow-up contrasts confirmed that, between 400-500 ms, old/new effects for the line encoding task were present only under exclusion instructions ($F(1, 20) = 11.47$, $MS_E = 9.04$, $p < .01$, $\eta_p^2 = .36$; Figure 25). Conversely, between 300-400 ms, a marginally reliable condition by retrieval instruction interaction suggested that old/new effects following the line encoding task were present only under inclusion instructions ($F(1, 20) = 3.87$, $MS_E = 11.75$, $p = .06$, $\eta_p^2 = .16$; Figure 24). A post-hoc test directly comparing these two old/new effects (i.e., as difference scores [old – new]) yielded a mean difference of $3.94 \mu V$, reflecting the opposing directions of the old/new differences in question (as seen by comparing the 3rd and 4th bars in the left panel of Figure 24 with the 5th and 6th bars in the right panel of Figure 25). This mean difference was statistically reliable ($t(20) = 4.13$, $SE = .95$, $p < .001$), suggesting that the ERP old/new effects following line encoding differed as a function of retrieval instructions. The same series of contrasts performed for old/new differences following animacy encoding yielded no reliable interactions ($F_s < 2.0$). Lastly, the three-way interaction present between 700-800 ms was not accompanied by any main effects or reliable lower-order interactions.

Effects of Study-Test Matching

To assess the affect of study-test matching on ERPs for recognized pictures, a series of Encoding Task (2: Animacy vs. Lines) by Retrieval Cue Type (2: Match vs. Exemplar) by Retrieval Instruction (2: Inclusion vs. Exclusion) by Electrode (4) ANOVAs were preformed separately for the anterior frontal, frontal, and parietal scalp regions during each of the six 100 ms intervals. No reliable effects of matching were found at any time interval over any scalp region.

Figure 24. Mean Voltage (μV) over the Frontal Scalp between 300-400 ms for Match Hits and Correct Rejections

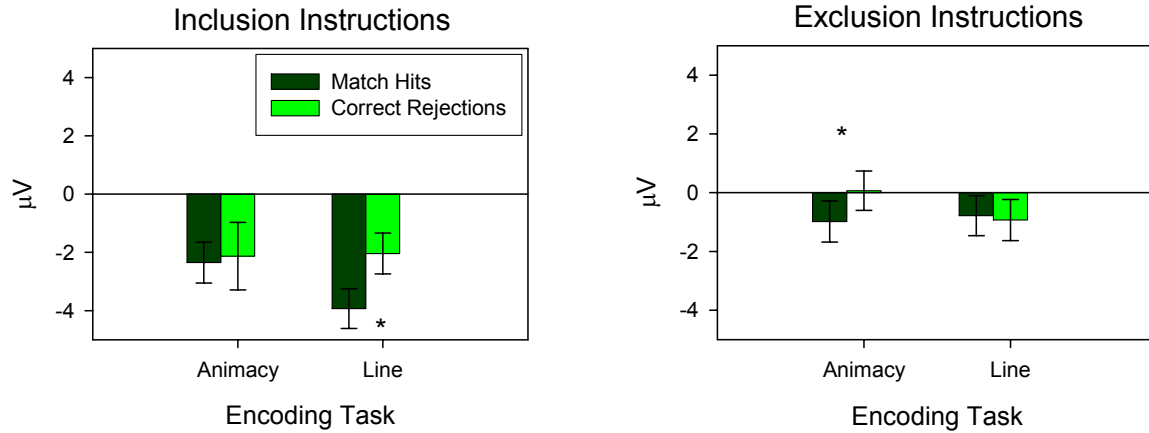


Figure 24. Error bars represent standard error of the mean. * $p < .05$, + $p \leq .07$.

Figure 25. Mean Voltage (μV) over the Frontal Scalp between 400-500 ms for Match Hits and Correct Rejections

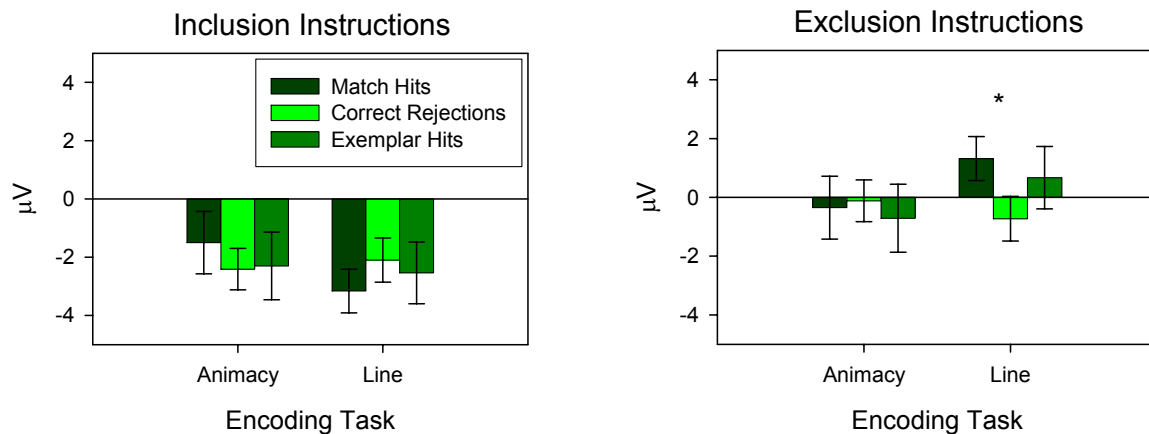


Figure 25. Error bars represent standard error of the mean. * $p < .05$, + $p \leq .07$.

Effects of Encoding and Retrieval Orientations on Hits and Correct Rejections

Hits. A Time Interval (6) by Encoding Task (2: Animacy vs. Lines) by Hit Type (2: Match vs. Exemplar) by Retrieval Instruction (2: Inclusion vs. Exclusion) by Electrode (4) ANOVA was performed. Encoding task by retrieval instruction ($F(1, 20) = 4.71$, $MS_E = 977.44$, $p < .05$, $\eta_p^2 = .19$) and encoding task by time interval ($F(1, 20) = 4.39$, $MS_E =$

7.73, $p < .01$, $\eta_p^2 = .18$) interactions were present and were accompanied by a retrieval instruction main effect ($F(1, 20) = 5.53$, $MS_E = 577.20$, $p < .05$, $\eta_p^2 = .22$). The encoding task by retrieval instruction interaction reflected the fact that, for recognized pictures encoded during the line task, the mean voltage between 200-800 ms was more positive for hits achieved under exclusion instructions than under inclusion instructions ($F(1, 20) = 10.58$, $MS_E = 5.63$, $p < .01$, $\eta_p^2 = .35$). The mean voltage between 200-800 ms for recognized pictures encoded during the animacy task did not differ as a function of retrieval condition ($F < 2.0$). The effect of retrieval condition observed for pictures encoded in the line task suggests the possibility that pictures encoded under a perceptual orientation are recognized differently when retrieval orientation is also perceptual versus when retrieval orientation is conceptual. The null effect of retrieval orientation for pictures encoded in the animacy task could be taken to suggest that conceptual encoding orientations lead to recognition that is agnostic with regard to retrieval orientation.

Correct rejections. A Time Interval (6) by Encoding Task (2: Animacy vs. Lines) Retrieval Instruction (2: Inclusion vs. Exclusion) by Electrode (4) ANOVA revealed no main effects or interactions. One simple effect of retrieval instruction was observed for pictures encoded in the animacy task, such that correct rejections in the inclusion condition were more negative going than correct rejections in the exclusion condition ($F(1, 20) = 4.56$, $p < .05$, $\eta_p^2 = .19$).

Topographic Dissimilarity Analyses. The results of the topographic dissimilarity analyses are shown in Figure 26. Between 200-800 ms, the topographies for animacy matching hits and correct rejections differed during four distinct intervals under inclusion instructions, 318-352 ms, 380-458 ms, 540-644 ms, and 668-800 ms

(Figure 26a, dark shading), and during two distinct intervals under exclusion instructions, 312-390 ms and 620-642 ms (Figure 26a, light shading). The topographies for animacy exemplar hits and correct rejections differed during six distinct intervals under inclusion instructions, 200-240 ms, 288-330 ms, 482-500 ms, 620-656 ms, and 782-800 ms (Figure 26b, dark shading), and during one interval under exclusion instructions, 598-622 ms (Figure 26b, light shading).

The topographies for line matching hits and correct rejections differed during four distinct intervals under inclusion instructions, 222-256 ms, 318-376 ms, 636-676 ms, and 784-800 ms (Figure 31c, dark shading), and during four intervals under exclusion instructions, 200-230 ms, 412-432 ms, 638-744 ms, and 778-800 ms (Figure 26c, light shading). The topographies for line exemplar hits and correct rejections differed during four distinct intervals under inclusion instructions, 226-266 ms, 300-384 ms, 428-442 ms, 470-482 ms (Figure 26d, dark shading), and during three intervals under exclusion instructions, 504-678 ms, 696-750 ms, and 764-796 ms (Figure 26d, light shading).

The topographic dissimilarity analyses show that the old/new ERP differences observed between 300-400 ms over the parietal scalp were accompanied by topographic differences between hits and correct rejections for the matching and exemplar animacy pictures under exclusion instructions, and for old/new differences between 400-500 over the frontal scalp for both matching and exemplar animacy pictures under inclusion instructions and for matching line pictures under exclusion instructions. In addition, topographic differences were also accompanied old/new ERP differences observed between 600-700 ms over the frontal scalp for matching and exemplar animacy pictures under exclusion instructions, and matching line pictures under inclusion instructions.

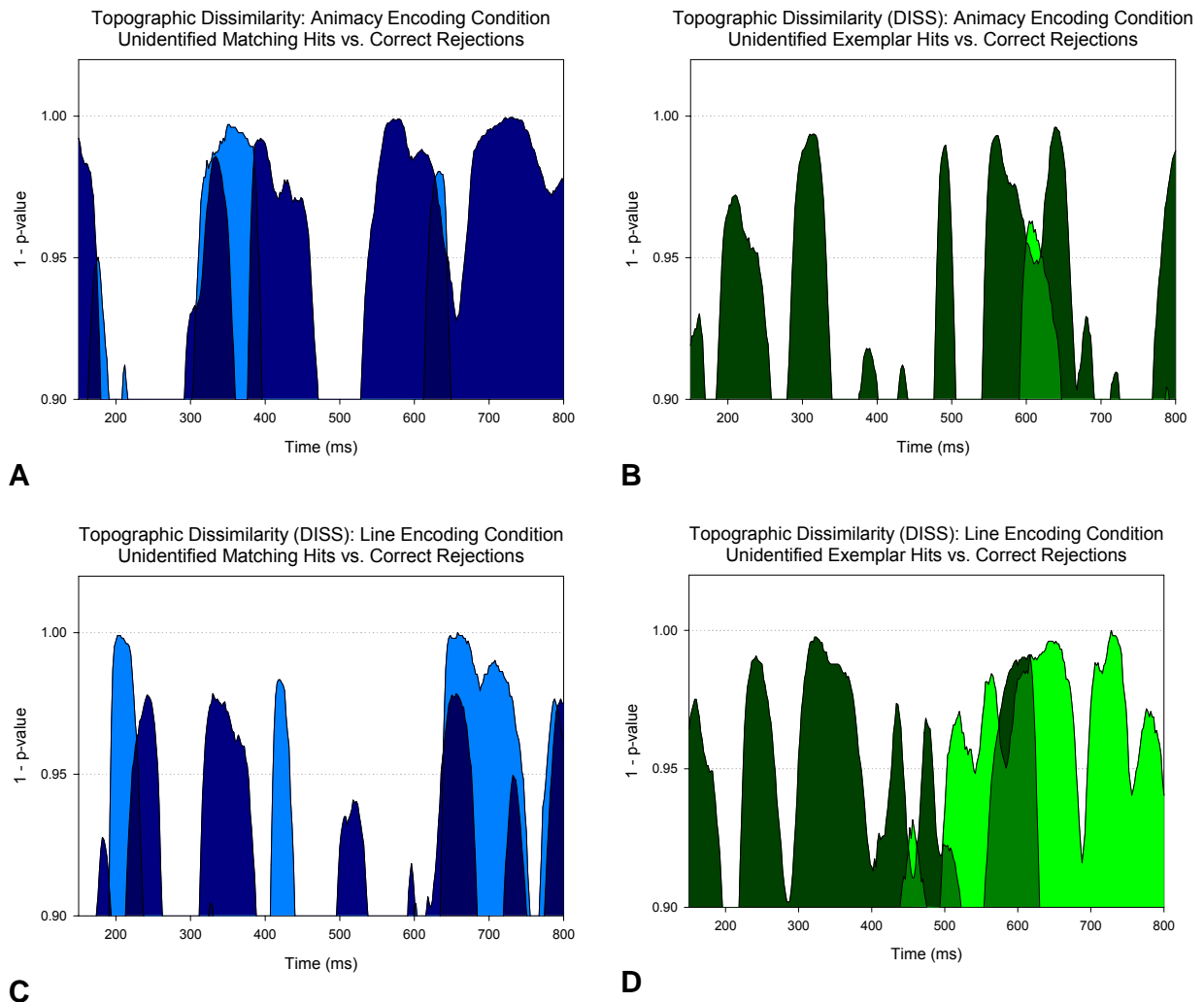
Figure 26. Topographic Dissimilarity Analyses for Retrieval ERPs

Figure 26. Topographic dissimilarity analysis of ERPs recorded during the retrieval phase of Experiment 2. On the y-axis, 1 minus p-values greater than 0.95 indicate statistically reliable differences between the ERP scalp topographies of the conditions being compared. Panels A and B show topographic dissimilarity profiles for pictures encoded in the animacy task, and Panels C and D show topographic dissimilarity profiles for pictures encoded in the line task. The color scheme for the shaded profiles is as follows: Light blue = exclusion/matching (A and C), dark blue = inclusion/matching (A and C), light green = exclusion/exemplar (B and D), dark green = inclusion/exemplar (B and D).

Discussion of Experiment 2

To summarize the results of the electrophysiological data recorded during encoding, the differences between ERPs were primarily between identified hits and unidentified misses, although differences were present between unidentified hits and misses, and between hit types. Moreover, the ERP differences were present only for the animacy encoding condition. It is unlikely that the differences between hits and misses over the frontal scalp were predictive of later recognition (i.e., Dm effects). This is in part because subsequent recognition effects typically emerge over the mid-frontal to mid-central scalp around 400 ms (e.g., Duarte et al., 2004; Otten & Rugg, 2001) with hits being more positive than misses. The differences between hits and misses observed here occurred between 200-600 ms over both mid-frontal and bilateral-parietal scalp, with hits being more positive than misses over the frontal and central scalp, and with misses being more positive than hits over the parietal scalp. It is more likely that the differences observed here reflect the N_{CL} (200-300 ms) and the N350 (400-500), which reflect processes related to closure and identification (respectively) and are not predictive of subsequent recognition memory. The N_{CL} was present to the same degree for both identified and unidentified hits in the animacy condition, whereas the N350 was present to the same degree for both unidentified hits and misses. Topographic differences were also observed between both identified and unidentified hits compared to misses during the latency of the N_{CL} . Likewise, topographic differences were also present between both unidentified hits and misses compared to identified hits during the latency of the N350. The topographic differences suggest qualitative, in addition to quantitative, differences in the neural activity for these components and their respective conditions.

For the animacy encoding condition, these results suggest that both identified and unidentified pictures that were subsequently recognized on the memory test achieved perceptual closure, and did so to the same degree, replicating the results of Experiment 1. Also consistent with the results of Experiment 1, subsequently recognized unidentified pictures (hits) and subsequently forgotten pictures (misses) underwent a more extensive search of the structural description system (object model selection stage) compared to subsequently recognized identified pictures, as indexed by the N350.

However, unlike in Experiment 1, the search of the structural description system appeared equally extensive for unidentified hits and misses. It is possible that instructing participants to determine whether a briefly presented, masked picture depicts a living or a non-living object changes how they encode the image, possibly reducing the amount of perceptual detail that is extracted relative to when participants are merely asked to name the picture. As a result, object model selection may be more difficult for unidentified pictures. This would presumably lead to a less diagnostic information being stored in the memory trace, should lead to worse memory on a subsequent test.

Indeed, a comparison of the behavioral indices of recognition memory between Experiment 1 and Experiment 2 bears out this prediction. The variables of retrieval instruction and test cue (matching, exemplar) in the animacy encoding condition of Experiment 2 and the variable of test cue (match, mirror reversed) in Experiment 1, mean old/new discrimination scores ($M = 0.28$, $SD = 0.26$, and $M = 0.46$, $SD = 0.40$, respectively) were subjected to an independent-samples t-test. The results showed that recognition memory was worse when participants assessed the animacy status of pictures in addition to attempting to identify them during encoding compared to when

they only attempted to identify the pictures ($t(58) = 2.04$, $SE = .09$, $p < .05$). Incidentally, when recognition memory from Experiment 1 was compared to recognition memory following line encoding in Experiment 2 ($M = 0.56$, $SD = 0.46$), no reliable difference was observed ($t(58) = 1.03$, ns). Thus, in considering the ERP encoding data and the behavioral retrieval data together, the suggestion is that animacy encoding in Experiment 2 resulted in less successful processing of unidentified pictures, such that despite subsequently recognized unidentified pictures undergoing perceptual closure, object model selection was less successful, which lead to poorer behavioral indices of recognition memory.

The relationship between the ERP encoding data and the behavioral data corresponding to the unidentified pictures in line encoding task is less straightforward. Again, no reliable differences in the ERPs at encoding were observed, and yet the behavioral index of recognition memory exceeded that of recognition memory in the animacy condition of Experiment 2 as well as that of Experiment 1. As described previously, ERPs to subsequent misses were generally reduced in amplitude during the intervals corresponding to the object identification components of interest (N_{CL} : 200-300 ms, N_{350} : 300-500 ms), while the ERPs to subsequent hits did not differ during the key intervals relative to the ERPs during the animacy task. This effect of encoding task on misses exclusively could very well have obscured any effects of interest that were present. For example, based on the results of Experiment 1 and the those found for the animacy task in the present experiment, the expected out come between 200-300 ms over the parietal scalp region would have been equivalent mean voltages for ERPs to identified and unidentified subsequent hits, and less negative ERPs to subsequent misses (i.e., an equivalent N_{CL} for identified and unidentified subsequent hits). Indeed,

subsequent hits did not differ from each other between 200-300 ms, consistent with the results of Experiment 1 and the animacy condition of the present experiment. However, because subsequent misses also did not differ from the two hit types, it is not possible to statistically verify the presence of the N_{CL} . A similar issue exists with confirming the N350, as confirmation involves statistical differences between subsequent hits and unidentified subsequent misses.

Subsequent memory have been shown to modulated encoding task (Otten & Rugg, 2001), and so the pattern of results reported here is not entirely unprecedented. However, in the case of Otten and Rugg (2001), both subsequent hits and subsequent misses differed between encoding tasks, with ERPs generally being more positive following animacy encoding relative to alphabetic encoding, primarily over the frontal region of the scalp. The present data is partially consistent with their results in that task differences were characterized by more positive-going ERPs over the frontal region of the scalp for animacy encoding. However, the difference between tasks was restricted to subsequent misses in the present study. There is no immediately obvious explanation for this finding. One possibility is that the line encoding task resulted in participants processing subsequently missed pictures differently than was the case in the animacy task. Perhaps as a result of participants orientation towards the perceptual aspects of the pictures, subsequently missed pictures were processed more similarly to subsequently recognized pictures than was the case in the animacy encoding condition, and therefore no ERP differences were present during encoding. If this were the case, then the improved memory following line encoding, as seen in the behavioral measure of memory, could have resulting from processing differences that were not observable with ERP, or were too small to detect.

Turning to the ERPs recording during retrieval, the main results were as follows. First, an FN400 (new more negative than old) was present over the frontal region of the scalp for matching pictures encoded in the line task and retrieved under exclusion instructions (perceptual/perceptual). Reversed old/new effects (old more negative than new) were present over the frontal region of the scalp during the latency of the FN400 (300-500 ms) for pictures encoded in the line and retrieved under inclusion conditions (perceptual/conceptual) and pictures encoded in the animacy task and retrieved under exclusion conditions (conceptual/perceptual). No reliable old/new effects were observed for pictures encoded in the animacy task and retrieved under inclusion instructions (conceptual/conceptual). An ANOVA contrasting the three statistically reliable old/new effects as differences scores (old – new) was significant ($F(2, 9) = 5.91, p < .05, \eta_p^2 = .56$). Follow-up tests showed that while the two reversed old/new effects were statistically equivalent in magnitude ($F(1, 10) = 1.60, ns$), both the reversed old/new effect observed between 300-400 ms for unidentified pictures encoded in the animacy task and retrieved under exclusion instructions ($F(1, 10) = 12.59, p < .01, \eta_p^2 = .56$) and the reversed old/new effect for unidentified pictures encoded in the line task and retrieved under inclusion instructions ($F(1, 10) = 11.20, p < .01, \eta_p^2 = .53$) differed from the FN400 observed between 400-500 ms for unidentified pictures encoded in the line task and retrieved under exclusion instructions.

Separate analyses of hits and correct rejections between 200-800 ms revealed that hits following the line task were more negative-going under inclusion instructions than under exclusion instructions, whereas hits following animacy encoding did not differ as a function of retrieval task. Conversely, correct rejections remained relatively consistent as a function of encoding and retrieval task, with the exception that correct

rejections in the animacy task were *more negative* under inclusion instructions than under exclusion instructions.

With respect to the animacy task, the greater negativity for correct rejections under inclusion instructions explains why (reversed) old/new effects were not observed for these trials and were for correct rejection trials under exclusion conditions. Note that hits following animacy encoding were not found to differ as a function of retrieval instructions, suggesting that the neural response to recognized pictures were similar across retrieval instructions. The fact that the neural response to non-studied pictures differed suggests that the lack absence of old/new effects for animacy inclusion trials does reflect a difference in memory processes, *per se*, but reflects instead a difference in how novel stimuli are processed as a result of the retrieval instructions.

Although correct rejections following line encoding did not differ as a function of retrieval instruction, hits did. This pattern, which is in some sense the opposite of what was seen following animacy encoding, may help to explain why an FN400 was present for pictures encoded in the line task and retrieved under exclusion instructions, and why reversed old/new effects were present under inclusion instructions. The fact the difference resided with hits and not correct rejections following line encoding suggests that the underlying processing difference is in fact memorial. That is, the way recognized pictures were processed following line encoding differed as a function of retrieval instruction, whereas novel pictures did not. Given that the difference is memorial, it is important to consider the ERP data from encoding (whereas it would not be important to do so if the differences were between correct rejections because correct rejections were not previously encoded). However, as described above, the interpretation of the ERPs from the line encoding condition are less than straightforward

given the fact that no differences were observed between conditions. Given these difficulties, further discussion of the ERP retrieval data is withheld until the General Discussion (which provides a broader context within which to interpret the data).

CHAPTER 8: GENERAL DISCUSSION

Summary

Using behavioral and electrophysiological measures, the research presented in this dissertation examined the contribution of perceptual and conceptual processes to familiarity-based recognition memory for pictures. The primary goal was to further clarify type of pictorial representations that support familiarity-based picture recognition. To examine familiarity-based picture recognition, pictures were masked and presented briefly to participants. On the basis of prior research (Gregg & Gardiner, 1994; Langley & Cleary, 2008), it was assumed that impoverished encoding would minimize the amount of recollection that would contribute to picture memory, and that pictures that could not be identified by name would be subsequently recognized on the basis of familiarity (Langley & Cleary, 2008).

To assess the type of pictorial representations likely to result from the impoverished encoding of pictures, ERPs were recorded as participants attempted to identify the briefly presented masked pictures. The ERPs were then examined for the components that prior studies have linked to specific stages of object identification (i.e., the N_{CL} and N350). The results from Experiments 1 and 2 showed an N_{CL} for subsequently recognized *unidentified* pictures that was equivalent in magnitude to that of subsequently recognized *identified* pictures. In addition, ERPs during the latency of the N350 differed between subsequently recognized identified and unidentified pictures. These results indicated that unidentified, masked pictures likely underwent successful “perceptual closure” (Bartlett, 1916) and a more effortful (and probably unsuccessful) object model selection process, resulting in the creation of a pictorial representation composed (at the very least) of a coherent global object structure that lacked the

sufficient perceptual detail necessary for it to be fully matched to stored object representations and consciously identified by name.

It is possible that the memory trace for the unidentified pictures contained coarse semantic information as well. If such semantic information were to reside in the pictorial memory trace, it would have likely been integrated during the object model selection process, as candidate object models and their corresponding conceptual attributes were activated and matched to the visual information extracted during the picture's presentation (Davies et al., 2004).

Familiarity-based recognition memory was assessed on the basis of a behavioral index of recognition of the unidentified pictures (d_a), and on the basis of the putative neural correlate of familiarity, the FN400, for recognized unidentified pictures. The behavioral and the electrophysiological indices of familiarity both implied greater familiarity-based recognition under conditions with the strongest orienting toward perceptual processing, suggesting a dominant role of perceptual information as evidence for familiarity-based memory judgments. However, above chance recognition was observed behaviorally under conditions that oriented participants toward conceptual processing at both encoding and retrieval (Experiment 2). In addition, (reversed) old/new effects were also observed under the conditions with the strongest orienting toward conceptual processing. These effects suggest that the familiarity-based RWPI observed in Experiments 1 and 2 did not rely solely on concrete perceptual representations that required an exact perceptual match between encoding and retrieval presentations. Rather, the data suggest that both perceptual and conceptual processing of pictures can support familiarity-based picture recognition. What is more, the data also suggest that the memory traces generated during encoding for the unidentified pictures

contain perceptual representations that are somewhat abstract in nature and are accompanied by limited conceptual knowledge that falls below the threshold necessary for conscious naming of the picture.

The Object Recognition and Visual Recognition

Memory Interface: An Emerging Field

Over the past 20 years, researchers in the cognitive sciences have lain witness to the gradual convergence of two literatures material to this dissertation: the object identification literature and the recognition memory literature. The syncretization of these disciplines has emerged in the midst of a larger trend concerning the synthesis of the vision and memory literatures, which until the 1990s remained considerably disparate (see Buckley & Gaffan, 2006). Presently, there is considerable interest among cognitive scientists in understanding how visual knowledge is represented, and how such representations contribute to long-term memory. This fact was acknowledged during the 50th Annual Meeting of the Psychonomic Society in November of 2009, where the first symposium on the topic was held (entitled, *Visual Knowledge: Emergence of a New Discipline that Synthesizes Vision and Memory Theory*).

Much of the research devoted to clarifying the relationship between visual perception processes and memory processes has focused on identifying shared brain structures. For example, lesion studies in animals conducted during the late 1970's and 1980's revealed a role of the hippocampus (e.g., Mishkin, 1978; Murray & Mishkin, 1984) and parahippocampal region (e.g., Murray & Mishkin, 1986; Zola-Morgan, Squire, Amaral, & Suzuki, 1989) in visual recognition memory for objects. Later research conducted during the 1990's and 2000's implicated these structures in object identification and visual perception (Buckley & Gaffan, 1997, 1998; Buckley et al., 2001;

Bussey et al., 2001, 2002, 2006; Devlin & Price, 2007; Murray & Bussey, 1999; Suzuki, Zola-Morgan, Squire, & Amaral, 1993; Tyler et al., 2004). Relative to its role in recognition memory, the role of the hippocampus in visual perception is currently unclear (Graham, Barense, & Lee, 2010). However, there are many empirical reports that provide evidence for the idea that the neuroanatomical apex of visual and recognition memory processes is the perirhinal cortex and surrounding cortical areas (e.g., entorhinal cortex; Buckley & Gaffan, 2006; Cohen, Poldrack, & Eichenbaum, 1997; Tyler et al., 2004). Indeed, numerous studies have linked the origins familiarity-based visual recognition to the perirhinal cortex (Bussey & Winters, 2005; Murray & Bussey, 1999), and the extant perirhinal cortex models provide a rich context within which to consider the data reported in this dissertation. In what follows, I discuss models of the perirhinal cortex and the type of representations that this structure houses. The role the perirhinal cortex plays in object encoding and retrieval is discussed, and the data from Experiments 1 and 2 are considered within this context.

The Perirhinal Cortex

Before describing the type of representations housed in the perirhinal cortex, it is important to first consider the type of information that the perirhinal cortex receives, and where this information is received from. I first consider the role of the perirhinal cortex in visual cognition, and then its known role in mnemonic processes.

Inputs and representations. In primates, the perirhinal cortex is physically located within the inferior medial temporal lobe, adjacent to the hippocampus, and parahippocampal and entorhinal cortices. The perirhinal cortex is also located at the tail end of the visual ventral stream construct (Desimone and Ungerleider, 1989), which is comprised of brain regions that are critical for processing various aspects of object

identity. Structures within the ventral stream, including the perirhinal cortex, are thought to house visual object features in a storage network dubbed the “perceptual representation system” (PRS; Tulving and Schacter, 1990). The PRS is known to contribute to perceptual learning and various memory functions (Cooper, Schacter, Ballesteros, & Moore, 1994).

As reviewed by Brown and Eldridge (2007), the perirhinal cortex receives a large proportion of its visual input from the von Bonin and Bailey (1947) ventral temporal areas TE (also see Saleem & Takana, 1996) and TEO, which together comprise the inferior temporal (IT) cortex. Areas TE and TEO receive input primarily from the visual cortex, thereby making their contributions to the perirhinal cortex almost exclusively visual.

It is well established that both TEO and TE represents object features that are important to object identification (such as shape, color, and texture; see Tanaka, 2004), while only coarsely coding for features less important to object identification, such as an object’s exact position (Lueschow et al., 1994; Gross & Mishkin, 1977), size (Lueschow et al.; Sary & Vogels, 1993), and luminance. In other words, these areas (particularly area TE) do not code for object attributes that are view-specific or immaterial to object identity (Tanaka, 2004), and therefore may only provide view-independent visual object information to the perirhinal cortex.

Area TE has also been characterized as representing the history and meaning of complex object features in a behavioral context (Ungerleider & Pasternak, 2004), a characterization supported by the observation that a greater proportion of TE neurons respond to familiar objects than to unfamiliar objects (Kobatake, Wang, & Takana, 1998). Thus, TE provides the perirhinal cortex not only with information regarding the

view-invariant visual properties of objects, but also with some information relevant to an object's prior occurrence (or its novelty).

Many models of ventral visual pathway structures posit that it represents visual information in a hierarchical fashion (Ungerleider & Pasternak, 2004), with the most primitive object features represented in caudal regions of the ventral pathway (closest to V1) and with the most complex features and feature configurations represented in rostral regions of the ventral pathway (closest to the perirhinal cortex); areas TE and TEO are on the more complex end of the hierarchy. Thus, a prominently held view of the perirhinal cortex is that it represents information about how features within an individual object relate to each other, as opposed to representations of individual features or representations of entire objects. Much of the data supporting this view has come from Bussey and colleagues (Bussey et al., 2001, 2002, 2006; Bussey & Saksida, 2002, 2005, 2007), who have shown that lesions to the perirhinal cortices of rats and macaques result in a number of impairments in recognizing and discriminating between objects, including the retention of learned visual discriminations, learning the configuration of individual novel objects, and the ability to learn new visual discriminations between objects.

The perirhinal cortex additionally receives input of other modalities, including auditory (superior temporal gyrus) and somatosensory (insular cortex), which suggests that perirhinal representations may be polymodal as opposed to entirely visual. Other prominent polymodal input contributors include association areas, such as the parahippocampal and entorhinal cortices, the prefrontal and cingulate cortices, and the superior temporal sulcus (Brown & Eldridge, 2007). The fact that the perirhinal cortex has connections to these brain regions further suggest that its representations not

entirely visual. Thus, it would appear that the role of the perirhinal cortex in visual object identification (visual processing more generally) is to integrate object features from various sensory domains into polymodal conjunctions.

As mentioned, the perirhinal cortex is just one of many structures comprising the MTL. Traditionally, the MTL was viewed as a brain module largely tasked with controlling declarative memory processes (Squire and Zola-Morgan, 1991). Thus, given the perirhinal cortex's location within the MTL, it has long been implicated in memory processes (e.g., Brown & Aggleton, 2001; Brown & Xiang, 1998; Zola-Morgan, Squire, and Amaral, 1989). Direct evidence for role of the perirhinal cortex in long-term explicit memory has been reported many times over (e.g., Montaldi et al., 2006). The most compelling of these reports are those that show strong linear relationships between perceived familiarity strength and perirhinal cortex activity, with no concurrent correlation between perceived familiarity strength and hippocampal activity (e.g., Montaldi et al., 2006). While the role of the hippocampus in explicit memory is indisputable, recent research converges on the notion that the hippocampus may be more directly involved relational/associative memory (or recollection; e.g., Davachi & Wagner, 2002) or in binding item and context information (Diana, Yonelinas, & Ranganath, 2007; Eichenbaum, 2007). According to such theories (e.g., Diana et al.), encoding context and spatial information is stored by the parahippocampus and item information is stored by the perirhinal cortex. It bears emphasis that the perirhinal cortex has reciprocal connects with the parahippocampus, but has no direct or reciprocal connections to the hippocampus proper. However, it likely receives indirect hippocampal input through both the entorhinal and parahippocampal cortices, which both maintain reciprocal connections with the hippocampus (Brown & Eldridge, 2007). It follows that the

perirhinal cortex may therefore receive input indirectly regarding object attributes represented by adjacent structures, such as spatial features and encoding context (Graham et al., 2010). Thus, it would seem improbable for the perirhinal cortex to solely represent feature conjunctions.

Perirhinal contributions to familiarity. As just described, the perirhinal cortex sits at the interface of two systems, one visual (the ventral visual stream; Desimone and Ungerleider, 1989) and one mnemonic (MTL memory system; Squire and Zola-Morgan, 1991). Thus, the assumption that the perirhinal cortex is critical to visual memory is appealing on both a logical and an intuitive basis. This assumption is supported by many of aforementioned studies that show the direct contribution of the perirhinal cortex to perception and memory processes. Moreover, the assumption that the perirhinal cortex plays a major role in visual memory has served as a foundation for many models of perirhinal cortex functioning, most of which generally agree on the nature of the representations that it stores (i.e., complex feature conjunction;). The questions most relevant to this dissertation concerns how these models explain object encoding and retrieval processes within the perirhinal cortex and the extent to which these explanations can account for the data from Experiments 1 and 2. In what follows, I describe a recent model of familiarity processes in the perirhinal cortex proposed by Volodya et al. (2008). The discussion then returns to the data from Experiments 1 and 2, which are considered with perirhinal cortex model so as to provide a richer context in which to interpret the data.

A central premise of Volodya et al.'s (2008) model is that familiarity is a first step toward retrieving context-dependent memory. Using the terminology introduced by Mandler (1980; see Chapter 2), Volodya et al. equate item *recognition* with familiarity-

based memory and *identification* with context-dependent memory. This articulation of the processes that contribute to recognition memory (familiarity and recollection, respectively) is well suited on conceptual grounds for interpreting the data reported in this dissertation. That is, in using Mandler's terminology, familiarity-based memory is by definition '*recognition*' without '*identification*'. Given that the type of memory of interest is that of recognized pictures that were not identified (assumed to be familiarity-based), the mapping between the model and the data is straight forward.

Volodya et al.'s (2008) account of familiarity processes in the perirhinal cortex begins by emphasizing that the phenomenological experience of familiarity implies only that one can distinguish between novel and previously encountered stimuli. That is, feelings of familiarity do not include reference to context, nor does it specify the type of information (i.e., evidence) on which the feeling of familiarity is based. According to Volodya et al.'s model, this undifferentiated familiarity in the perirhinal cortex is initially signaled as a decrease in response to previously encountered visual stimuli, whereas novel stimuli elicit an increase in neural activity. Volodya et al. suggest that the neural responses in the perirhinal cortex to familiar and novel stimuli are mediated in a top-down manner by particular regions of the prefrontal cortex (i.e., anterior cingulate, orbitofrontal cortex, and ventromedial cortex). Support for this notion has come from past research that has demonstrated marked impairments to recognition memory when the perirhinal cortex is disconnected from the prefrontal cortex through lesion (Parker & Gaffan, 1998), and studies showing an *increase* in activity to familiar, as opposed to novel stimuli in the prefrontal cortex (see Xiang & Brown, 2004). As such, it is the activity in the prefrontal cortex that produces the observable familiarity signal in the Volodya et al. model, not the perirhinal cortex.

Xiang and Brown (2004) have suggested that the functional significance of the prefrontal activity is one of a retrieval mechanism that conveys information about familiar stimuli. Volodya et al.'s model is consistent with this interpretation, but they argue for a more specific role of the prefrontal cortex. Namely, they argue that the prefrontal activity reflects "readout" (recovery and interpretation of perirhinal cortex representations), which is based on a global-matching-like process (Clark and Grounlund, 1996; see Chapter 2) that non-selectively samples the entire excitatory network. In other words, the increase in prefrontal activity is thought to reflect the "match" between what is seen and the representations stored in memory. Volodya et al. argue further that the matching process accumulates *evidence* about the significance of a particular stimulus, which in turn, through feedback to the perirhinal cortex, facilitates the potentiation of those synapses that are selective for the stimulus in question. Given sufficient potentiation of a group of neurons that together represent an object, the strengthened synapses will come to constitute a recallable memory.

To review, many studies suggest that the perirhinal cortex contributes to both the encoding/identification of objects (Bartko et al., 2007; Buckley & Gaffan, 2006; Bussey & Winters, 2005; Murray & Bussey, 1999; Meunier, Bachevalier, Mishkin, & Murray, 1993; Murray et al., 2007; Preston et al., 2010; Staresina & Davachi, 2008; Winters et al., 2008) and the retrieval of object representations from long-term memory (Barens, Gaffan, & Graham, 2007; Bussey & Saksida, 2002, 2005, 2007; Bogacz, Brown, & Giraud-Carrier, 2001; Cohen, Poldrack, & Eichenbaum, 1997; Cohen et al., 1999; Davies et al., 2004; Graham et al., 2010; Meunier, Bachevalier, Mishkin, & Murray, 1993; Rolls et al., 2005; Ryan et al., 2000; Volodya et al., 2008; Xiang & Brown, 2004). Of particular relevance to this dissertation are the several studies that have explicitly

shown that activity in the perirhinal cortex during encoding is predictive of subsequent *familiarity-based* recognition (as opposed to recollection-based recognition), and in most cases its contribution has been observed with no accompanying contribution from the hippocampus (Davachi, Mitchell, & Wagner, 2003; Dougal, Phelps, & Davachi, 2007; Kensinger & Schacter, 2006; Preston et al., 2010). In light of the aforementioned research, it seems clear that what is known about the representations of stored in the perirhinal cortex should greatly inform the question central to this dissertation: What types of information can serve as evidence for familiarity-based recognition?

Can Perirhinal Functioning Explain the Data?

The extant literature on the subject is fairly consistent in its suggestion that the perirhinal cortex represents the conjunctions of object features (Barense et al., 2007; Bussey & Saksida, 2002, 2005, 2007; Bussey et al., 2006; Cowell et al., 2006; Danckert, Gati, Menon, & Köhler, 2007), and in all likelihood it also less prominently represents some non-visual information (Brown & Eldridge, 2007; Davies et al., 2004; Lee, Levi, Davies, Hodges, & Graham, 2007). Given what is known about the perirhinal cortex's role in both encoding and retrieval related aspects of familiarity, a number of predictions can be made about how familiarity-based object memory should behave in response to manipulations of the perceptual processing of pictures and objects, assuming familiarity were to rely largely on this medial temporal structure. Moreover, should the data from Experiments 1 and 2 align with some of these predictions, it could provide additional (albeit indirect) evidence concerning the type of evidence supporting recognition of unidentified pictures.

The behavioral data. To my knowledge, there are some predictions of the perirhinal cortex model (generally speaking) that are implied by the existing literature,

but that have yet to be formally tested. For example, Tyler et al. (2004) showed that the level of activation within the perirhinal cortex varied with the degree of detail that participants had to extract from an object during encoding. In an fMRI study, Tyler et al. had participants perceptually identify pictures of objects and animals either on a “domain level” (*living or manmade*) or on a “basic level” (*name the picture, e.g., horse or phone*). The fairly simple prediction was the perirhinal cortex activation would be greatest when participants performed “basic level” identification, because it required participants to make a finer-grained differentiation between objects (e.g., *pen vs. pencil*), as opposed to the less precise decision inherent to a “domain level” identification (e.g., *bottle vs. puppy*). As predicted, the results showed greater perirhinal activation during the “basic level” identification. This suggests that task demands at study can modulate the contribution of the perirhinal cortex to picture encoding, such that more complex analyses (or more perceptually demanding tasks) lead to greater perirhinal activity. This finding is consistent with some models of the perirhinal cortex, which assume that the perirhinal cortex is most likely to be engaged when a task is difficult, or when the features of the stimulus generate uncertainty (or ambiguity) with respect to the decision that must be made (e.g., Bussey & Saksida, 2002, 2005, 2007; Bussey et al., 2006; Cowell et al., 2006).

Although Tyler et al. (2004) did not report recognition memory accuracy for the identified pictures, perirhinal cortex models would predict greater memory for pictures identified at the “basic level” (due to the greater role of the perirhinal cortex), assuming that picture recognition memory were to be familiarity-based.

An alternative explanation for the hypothetical outcome of Tyler et al.’s study could be that memory performance should be better merely because making a “basic

level” identification (determining the name of an object) requires more complete processing of the stimulus, or requires more attentional resources than would a “domain level” identification. In other words, the stimulus would be processed on a “deeper” level (Craik & Lockhart, 1972).

The data from Experiment 2 can distinguish between these two accounts—a perirhinal cortex explanation versus a size congruency explanation. Recall that participants in Experiment 2 encoded pictures under two conditions: The animacy task (*living or non-living*) and the line task (*are there more horizontal or vertical lines?*). For unidentified pictures, which were recognized on the basis of familiarity, perirhinal cortex models would predict better recognition of the pictures encoding during the line task. This is the case because the line task required participants to scrutinize each picture to determine whether it contained more horizontal lines or more vertical lines (not the case for the animacy task). Therefore, the task is more perceptually demanding and requires a more considered decision. Note that more traditional accounts of recognition memory, for instance, the size congruency framework (Craik & Lockhart, 1972), would predict the opposite pattern. That is, judging the animacy of an image would be considered a “deeper” (more semantic or conceptual) mode of processing as compared to judging the superficial features or structural properties of the picture (line task). As was reported in Figure 18, the data of Experiment 2 support the prediction of the perirhinal cortex model—recognition of unidentified pictures was superior for pictures encoded in the line task compared to pictures encoded in the animacy task.

The opposite pattern was true for identified pictures (Figure 18). That is, recognition memory was superior for identified pictures encoded during the animacy task, and worse for identified pictures encoded during the line task. It is assumed that

picture identified by name during encoding have a high potential for being recognized on the basis of both recollection and familiarity. While not critical for familiarity, the hippocampus, the fornix, and other neighboring structures are important for the encoding and recollection of experimental stimuli, as these structures are implicated in binding episodic details to the pictorial memory trace (e.g., spatial and temporal context, stimulus identity; Graham et al., 2010). If true, the role of the perirhinal cortex would be diminished according to Volodya et al.'s (2008) model because familiarity-based memory is only an initial step towards "identification" (i.e., recollection). When identification is achieved, context-dependent memory dominates, which does not rely on the perirhinal cortex or its conjunctive feature and its representations.

The behavioral data from Experiment 1 are also consistent with predictions of the perirhinal cortex in this regard. Specifically, the nature of the representations stored by the perirhinal cortex dictate that certain object features could be changed between study and test presentations without resulting in impairments to object recognition memory. As described earlier in this discussion, such properties include left-right orientation, size, luminance, and other features that are not critical to object identification. In contrast, recognition memory that relies on episodic representations would likely be impaired by such changes, as the episodic representation system codes for highly specific visual details (e.g., orientation, size, spatial position). Recall that in Experiment 1 there was no difference in memory for mirror reversed pictures that were unidentified at encoding (Figure 11). In contrast, memory for identified pictures was reliably poorer for mirror reversed pictures compared to matching identified pictures.

While far from definitive, the behavioral indices of recognition memory for unidentified pictures do agree with the predictions that could be made on the basis of

perirhinal cortex models of familiarity. Moreover, the behavioral data for unidentified pictures are inconsistent with predictions that could be made on the basis of episodic accounts of familiarity. Conversely, for Experiment 2, when encoding task was manipulated, the pattern of later recognition of unidentified pictures was consistent with perirhinal cortex model predictions, and inconsistent with episodic representation predictions.

Electrophysiological data. Interpreting the electrophysiological data within a perirhinal cortex model is not straight forward. However, there are a few correspondences that are worth noting with regard to the retrieval data. For example, according to Volodya et al.'s model the directly observable familiarity signal emerges not from the perirhinal cortex (which is likely too deep to record signals for at the scalp), but instead from the prefrontal cortex. The putative neural correlate of familiarity (FN400) has been observed over fronto-polar scalp regions on several occasions (e.g., Ecker & Zimmer, 2007; Groh-Bordin et al., 2005) as well as over the frontal scalp region, both of which area fairly near familiarity-related prefrontal areas. Another consistency concerns the FN400 recorded over the frontal scalp for unidentified line picture under exclusion conditions. The perirhinal cortex model would predict the strongest familiarity signal in the most perceptual orienting condition, which is what occurred in Experiment 2. In this regard, the behavioral data (showing the greatest familiarity following perceptual encoding) are at the very least consistent with the ERP data recorded at retrieval in that the indices of familiarity are largest in conditions maintaining a perceptual orientation.

Conclusions

In this dissertation it was shown that participants can recognize pictures at test that they did not identify during encoding, and that the recognition of such unidentified pictures is accompanied by the putative neural correlate of familiarity (Experiments 1 and 2). Moreover, it appears that familiarity-based picture recognition rely on non-episodic representation.

On the basis of the behavioral data and the electrophysiological data, it appears that participants can recognize unidentified masked pictures on the basis of perceptual and possibly conceptual information. However, Experiment 2 showed that perceptual orientation at encoding (behavioral and electrophysiological data) and retrieval (electrophysiological data) increases familiarity-based picture recognition. In general, the data suggest that familiarity (as observed within the context of Experiments 1 and 2) can show some degree of perceptual specificity, despite the fact that it likely it is supported by representations that are abstract. While it was not the goal of this research to identify brain structures involved in the recognition of unidentified pictures, it does appear likely that this form of picture memory relies on conjunctive feature representations housed in the perirhinal cortex.

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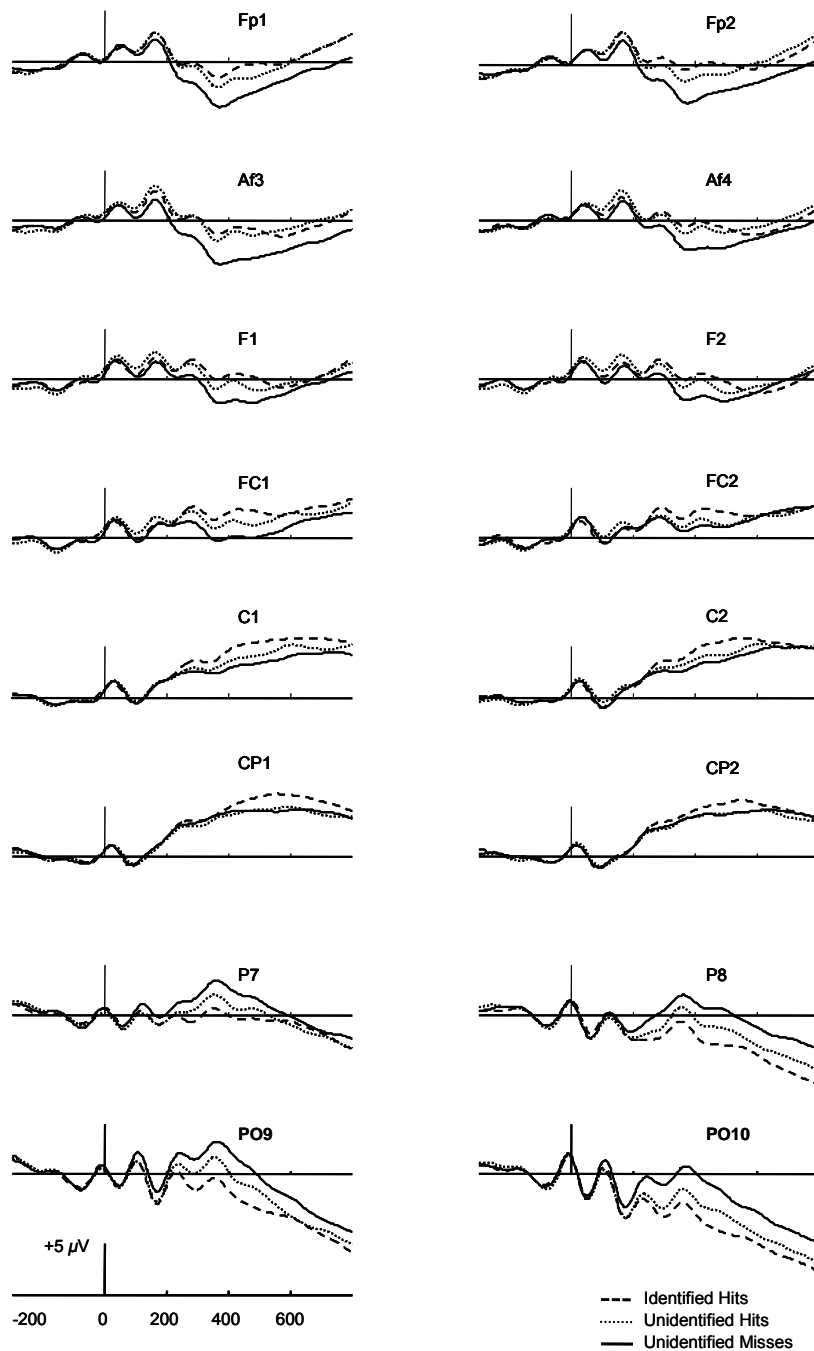
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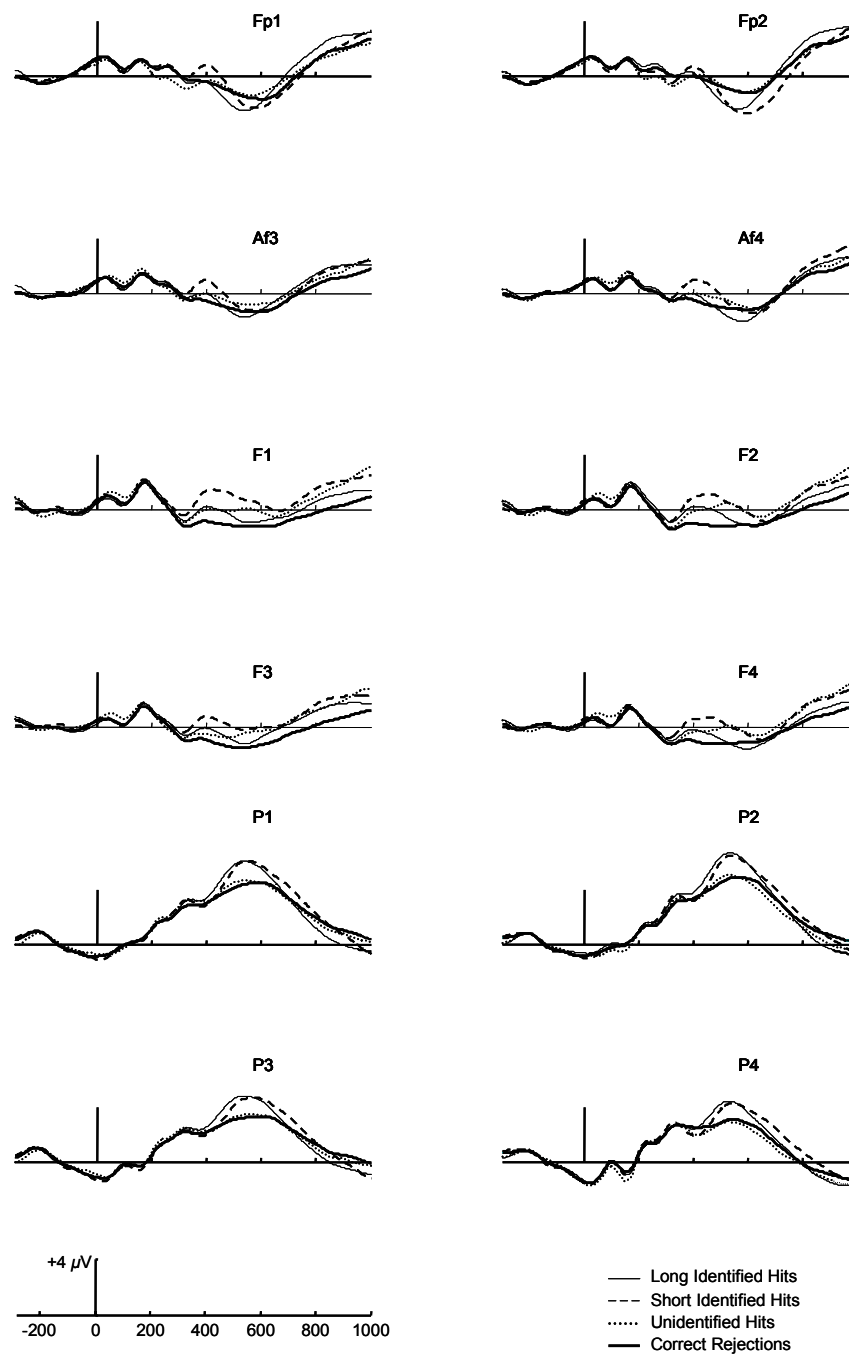
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APPENDIX A. TOPOGRAPHICALLY ARRANGED
GRAND AVERAGE ERP DATA – EXPERIMENTS 1 & 2

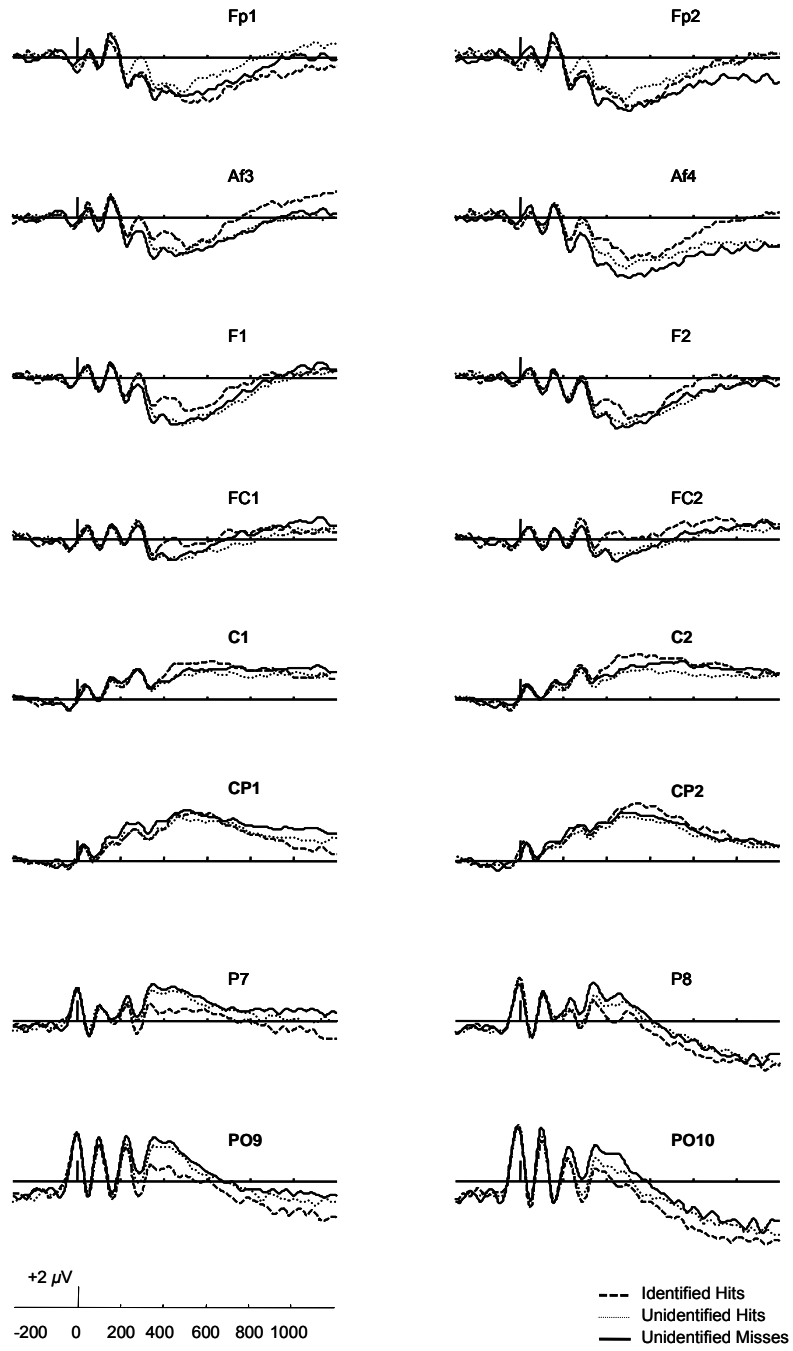
Experiment 1: ERPs during Encoding



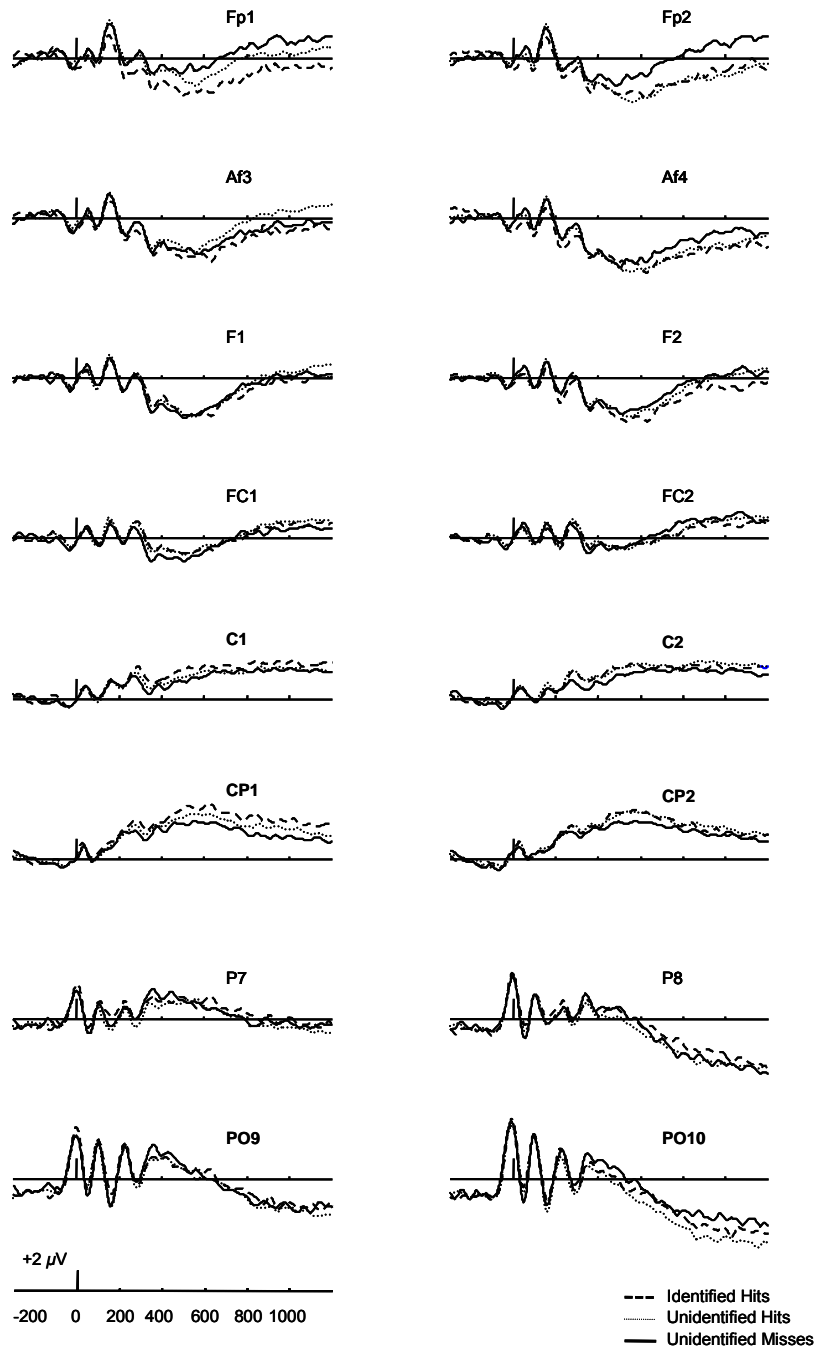
Experiment 1: ERPs during Retrieval



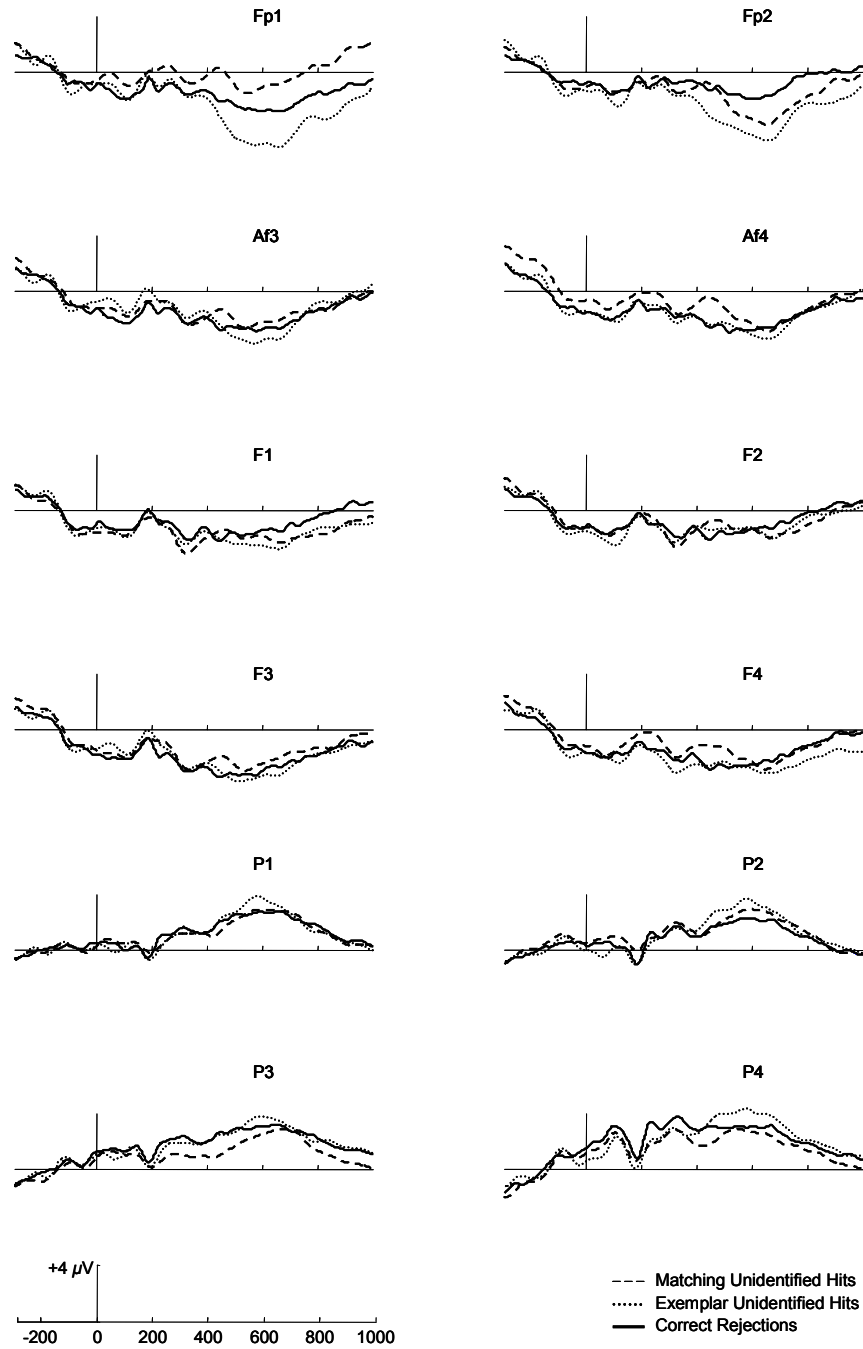
Experiment 2: ERPs during Animacy Encoding



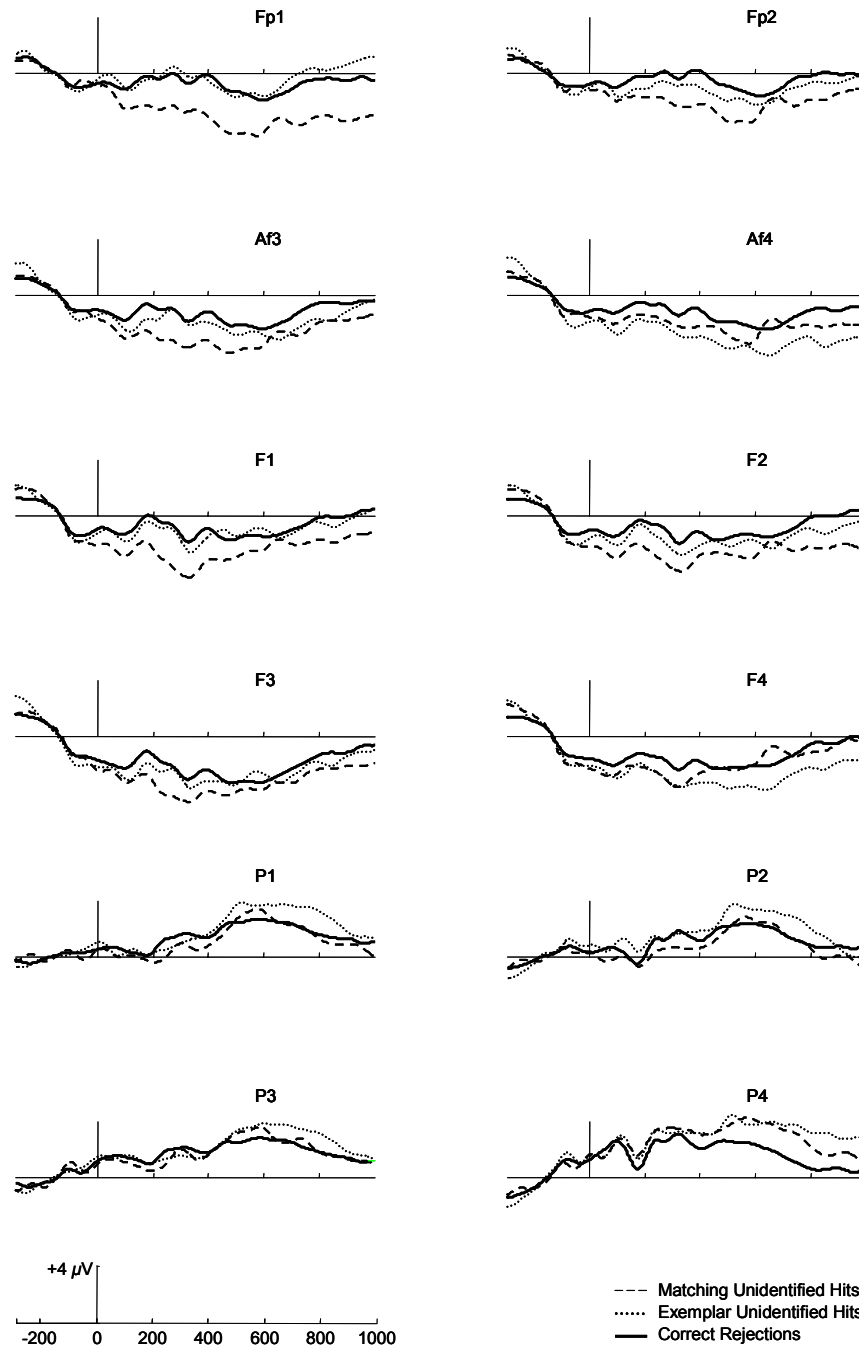
Experiment 2: ERPs during Line Encoding



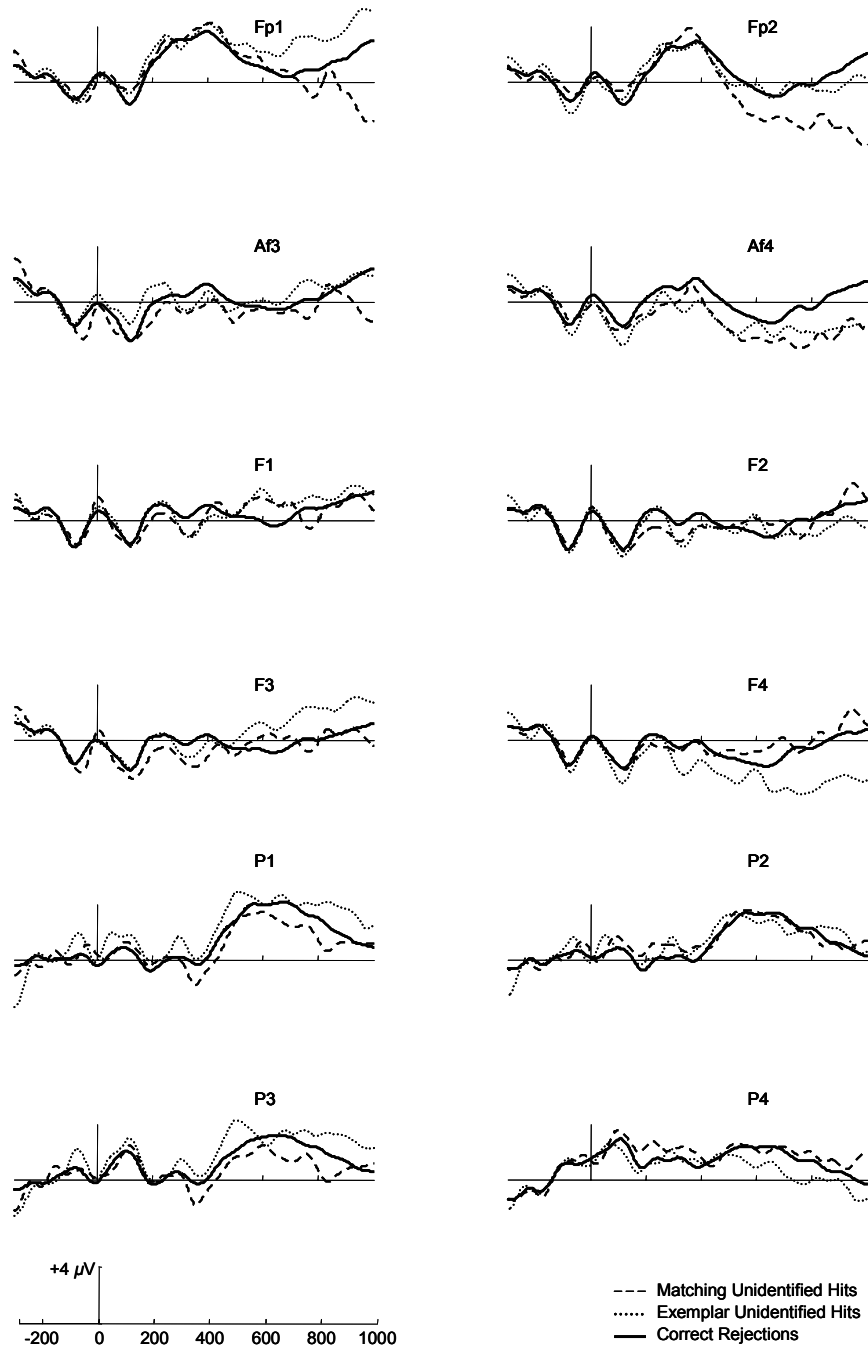
Experiment 2: ERPs during Inclusion Retrieval Instructions (Following Animacy Task)



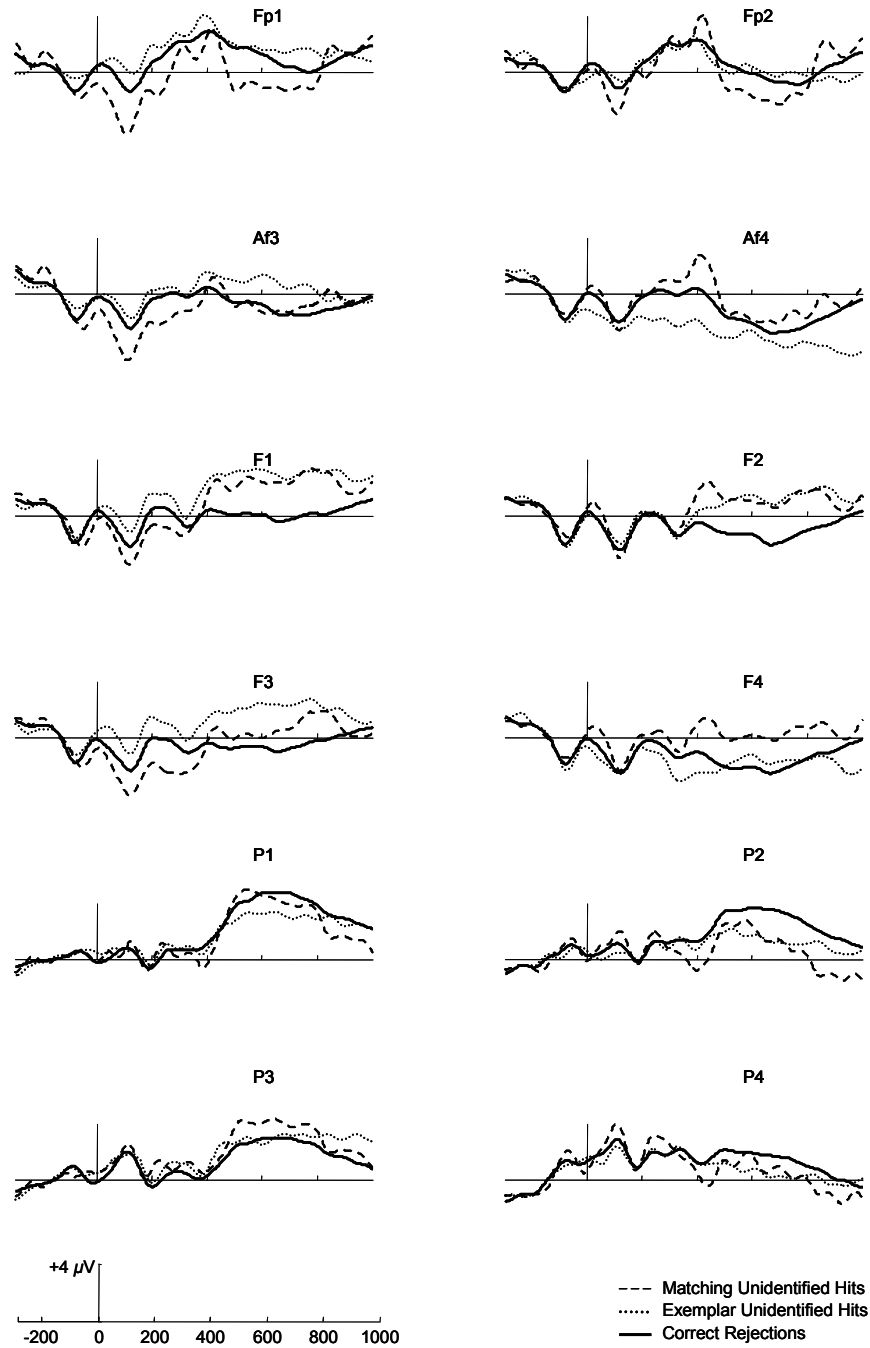
Experiment 2: ERPs during Inclusion Retrieval Instructions (Following Line Task)



Experiment 2: ERPs during Exclusion Retrieval Instructions (Following Animacy Task)



Experiment 2: ERPs during Exclusion Retrieval Instructions (Following Line Task)



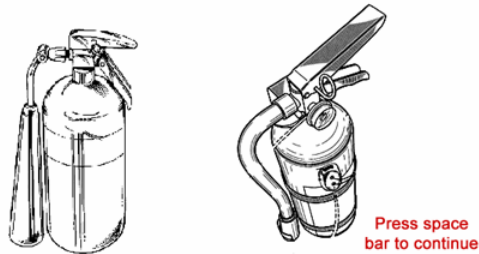
APPENDIX B. RETRIEVAL INSTRUCTION FOR INCLUSION AND EXCLUSION CONDITIONS

Inclusion Instructions

On the memory test, some of the pictures will be identical to the pictures that you've seen.

However, some of the pictures will only resemble pictures you've seen. That is, you may encounter a different instance of a picture that you've seen.

For this test, **you should call an object "old" even if it is not exactly the same as the object that you were briefly presented with.**

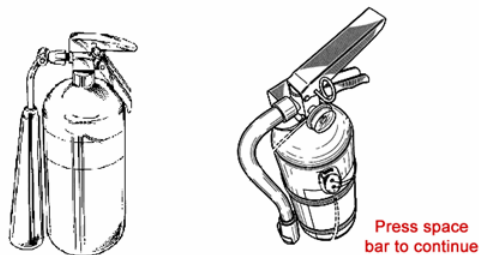


Exclusion Instructions

On the memory test, some of the pictures will be identical to the pictures that you've seen.

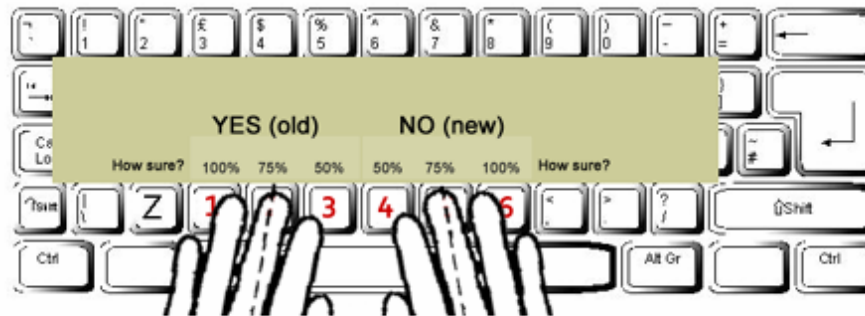
However, some of the pictures will only resemble pictures you've seen. That is, you may encounter a different instance of a picture that you've seen.

For this test, **you should *only* call an object "old" if it is *EXACTLY* the same as the object that you were briefly presented with.**



APPENDIX C. MEMORY TEST RESPONSE INSTRUCTIONS GIVEN DURING PRACTICE

How to respond during the memory test



If you are **highly confident** that the picture is old, **press 1**.

If you are **highly confident** that the picture is new, **press 6**.

Use the keys in between for lower levels of confidence