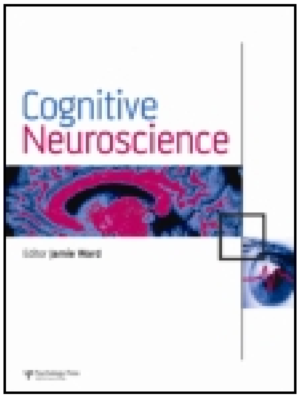


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# More than a feeling: Pervasive influences of memory without awareness of retrieval

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# Discussion Paper

# More than a feeling: Pervasive influences of memory without awareness of retrieval

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The subjective experiences of recollection and familiarity have featured prominently in the search for neurocognitive mechanisms of memory. However, these two explicit expressions of memory, which involve conscious awareness of memory retrieval, are distinct from an entire category of implicit expressions of memory that do not entail such awareness. This review summarizes recent evidence showing that neurocognitive processing related to implicit memory can powerfully influence the behavioral and neural measures typically associated with explicit memory. Although there are striking distinctions between the neurocognitive processing responsible for implicit versus explicit memory, tests designed to measure only explicit memory nonetheless often capture implicit memory processing as well. In particular, the evidence described here suggests that investigations of familiarity memory are prone to the accidental capture of implicit memory processing. These findings have considerable implications for neurocognitive accounts of memory, as they suggest that many neural and behavioral measures often accepted as signals of explicit memory instead reflect the distinct operation of implicit memory mechanisms that are only sometimes related to explicit memory expressions. Proper identification of the explicit and implicit mechanisms for memory is vital to understanding the normal operation of memory, in addition to the disrupted memory capabilities associated with many neurological disorders and mental illnesses. We suggest that future progress requires utilizing neural, behavioral, and subjective evidence to dissociate implicit and explicit memory processing so as to better understand their distinct mechanisms as well as their potential relationships. When searching for the neurocognitive mechanisms of memory, it is important to keep in mind that memory involves more than a feeling.

***Keywords:*** Implicit memory; Explicit memory; Recollection; Familiarity; Awareness.

So many people have come and gone
Their faces fade as the years go by
Yet I still recall as I wander on
As clear as the sun in the summer sky . . .

—Donald Scholz and Boston, *More than a feeling* (1976)

Life is enriched by the ability to conjure long-past episodes back to mind in vivid detail. Yet not all expressions of memory involve this experience of conscious recollection. Indeed, differences between recollection and another memory experience known as familiarity are often emphasized in contemporary

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memory research. The experience of familiarity is strikingly illustrated by the butcher-on-the-bus phenomenon, which occurs when an individual (such as your butcher) is encountered out of context (such as on a bus instead of in the butcher shop) and can be recognized but not identified (Mandler, 1980). Seeing the butcher in this circumstance triggers a strong feeling of knowing devoid of the contextual recollection that would be associated with successful identification. This acontextual familiarity arises with little or no effort, although further retrieval attempts may lead to recollection of past encounters in the butcher shop that would support identification. A substantial portion of memory research over the past 40 years has focused on the cognitive and neural characteristics of recollection and familiarity (Yonelinas, 2002). In many ways, this research has been revolutionary, as memory research prior to the cognitive revolution largely avoided consideration of subjective experience (Mandler, 2008). Efforts to identify the cognitive and neural bases of these experiences have produced many fundamental insights into the mechanisms of memory.

We contend that a recent overemphasis on recollection and familiarity, however, has caused much confusion and is impeding further progress. The chief downside of this recollection/familiarity focus is that forms of memory without awareness of retrieval have been relatively ignored. These nonconscious or *implicit* expressions of memory occur with behavioral, cognitive, and neural signatures that are reliably produced in many circumstances, despite the fact that individuals are generally unaware of their occurrence (Dew & Cabeza, 2011; Eichenbaum & Cohen, 2001; Schacter, 1987; Squire, 2004). As such, a near-exclusive focus on conscious, or *explicit*, expressions of memory, such as recollection and familiarity, has led to a gross oversimplification of the complex relationships between neurocognitive processing and subjective experiences. The immediate ramifications of this situation are distortions in our understanding of relationships between memory processing and memory experiences. Negative impacts are broadening as findings and methods from memory research are increasingly applied to other psychological variables. Accordingly, we argue that implicit memory must be given adequate consideration in cognitive neuroscience, in order to elucidate the complexity whereby neurocognitive processing gives rise to subjective memory experiences. Some of this processing also falls into the category of implicit memory processing and does not produce subjective experiences. Although subjective states such as recollection and familiarity are important, there is more than a feeling to consider when searching for the neurocognitive basis of memory.

In this review, we will first describe some of the negative impacts that have been spawned by an overemphasis on subjective memory experiences. We will then outline research that illustrates the broad reach of implicit memory processing, with a focus on results from experiments conducted in our laboratories. These findings and the methods used to achieve them have important ramifications for our understanding of the neurocognitive basis of memory and for the ways in which different memory processes can be characterized experimentally. Implicit memory processing can be difficult to characterize, but doing so is nonetheless important as this type of processing can influence behavior in ways that are powerful and under-appreciated. It is important to keep in mind what is at stake in the accurate identification of explicit and implicit mechanisms of memory. Although our review focuses primarily on the methodological issues involved in distinguishing memory mechanisms from the conscious awareness of memory, these general considerations are highly applicable to the attempt to identify causes for disrupted memory in many neurological disorders and mental illnesses. Indeed, our theoretical and methodological suggestions are highly relevant to ERP investigations of memory disruptions in conditions such as schizophrenia (e.g., Guillaume, Guillem, Tiberghien, & Stip, 2012) and Alzheimer's disease (e.g., Ally, McKeever, Waring, & Budson, 2009), and we therefore suggest a strong focus on the distinction between explicit and implicit memory processing in future studies on mechanisms for disrupted memory.

## BUTCHERING THE BUTCHER-ON-THE-BUS EXPERIENCE: THE OVERSIMPLIFICATION OF FAMILIARITY MEMORY

The subjective experiences of recollection and familiarity are relatively easy to identify; an individual relives past events when recollection is experienced and "knows" when only familiarity is felt. Methods such as the remember/know procedure are therefore sufficient to identify these experiences during memory testing (Yonelinas, 2002). Because these are such well-defined subjective states, it is tempting to think that uncovering the mechanisms (i.e., neural processing events) responsible for each state should be equally straightforward. However, this endeavor is far from straightforward if, as we contend, there is not a simple one-to-one mapping between the requisite neural events and experiences of either recollection or familiarity. The complexity of relationships between neural processing and subjective experience must not be overlooked. We do not dispute that subjective states can be linked to neural processing. Rather, we oppose the notion that recollection and familiarity will each be associated with, for instance, a particular neural signal, because this proposition oversimplifies the complex origins of subjective qualities. Indeed, despite tremendous efforts, the neural mechanisms responsible for even relatively simple experiences, such as conscious visual perception, are still poorly understood (Lau & Rosenthal, 2011; Leisman & Koch, 2009), and recollection and familiarity are far more complex. As described below, the neural processing that accompanies subjective experience in memory experiments depends on factors such as the context of the retrieval event, the nature of the retrieval cue, and other variables that are relatively unrelated to the experience itself. The operating principles of the neural systems that accomplish memory appear to be dictated by the nature of the representations that they support and the kind of computations performed on these representations rather than by the resulting subjective experiences (for other specific examples, see Cowell, Bussey, & Saksida, 2010; Eichenbaum & Cohen, 2001; Henke, 2010; Ranganath, 2010).

The realization that many forms of neurocognitive processing can be relevant to the subjective "end state" of retrieval is relatively well appreciated for recollection compared to familiarity. That is, there is a better appreciation in the field that recollection is likely multifaceted, varying in the type of neurocognitive processing responsible and the relevant brain regions and based on the content of the recollection experience. For instance, various findings have emphasized distinctions between retrieval processing generally relevant for episodic memory and neural activations specifically associated with recollection. To briefly summarize a substantial literature, various regions in prefrontal, parietal, and medial temporal cortex are implicated in various encoding and retrieval functions that support explicit memory, including recollection (Buckner & Wheeler, 2001; Eichenbaum & Cohen, 2001; Gabrieli, 1998; Simons & Spiers, 2003). In contrast, processing particularly related to recollection has been reported in the form of activity in some medial temporal regions, such as the hippocampus (Eichenbaum, Yonelinas, & Ranganath, 2007), as well as in primary sensory cortex (Danker & Anderson, 2010). It is especially intriguing that activity is observed in sensory-specific cortex in a manner consistent with the contents of the recollection experience. That is, olfactory cortex is active when recollection involves previously smelled odorants (Gottfried, Smith, Rugg, & Dolan, 2004), auditory cortex is active when recollection involves previously heard sounds (Goldberg, Perfetti, & Schneider, 2006), and so on, even when these modalities are not subject to external input during retrieval (i.e., no odorants or sounds presented). These sensory-specific effects have been reported for many stimulus categories (reviewed in Danker & Anderson, 2010), and are consistent with the notion that the specific regions of cortex responsible for originally experiencing an event are reactivated when that experience is recalled. Of course, there is much still to learn about the mechanisms for recollection. Nevertheless, attempts to account for recollection mechanisms generally appreciate the complexity of the relevant retrieval events. Recollection is not associated with a specific all-purpose neural correlate, but instead involves different kinds of neurocognitive processing depending on the exact nature of the recollection experience and the situation in which it is produced. A tacit appreciation of this complex relationship between the recollection experience and the neural processing responsible for it is demonstrated by the fact that it is not common for memory researchers to claim that recollection has occurred whenever "brain activation X" is observed in an experiment. That is, it is extremely unlikely that the *reverse inference* (Poldrack, 2006) of the recollection experience is based on some observed pattern of brain activity (in fact, we are aware of only a few such inferences in the literature). This is a good thing, given that even some fairly well-established "signatures" of recollection, such as activation of the hippocampus, have recently been shown to occur even in the absence of subjective awareness of memory (i.e., during implicit expressions of memory that do not involve the experience of recollection; Hannula & Ranganath, 2009; Rose, Haider, Salari, & Buchel, 2011). Indeed, some current theorizing suggests that recollection may be supported by automatic and implicit processing in the hippocampus, followed by the emergence of more widespread cortical interactions that support the subjective state of recollection (Moscovitch, 2008), although some evidence indicates that the second stage of this retrieval process need not follow the first (e.g., Hannula & Ranganath, 2009). In sum, recollection is too complex to be reduced to a one-to-one relationship with a particular neural signal or brain structure.

In contrast, overly simplistic accounts of familiarity are common. At some level, this is not surprising given the definition of the familiarity experience: Familiarity is a feeling of knowing that is devoid of the contextual detail that, if present, would be experienced instead as recollection. Therefore, familiarity is defined primarily in opposition to recollection. Indeed, the vast majority of relevant neuroimaging investigations identify neural signals of familiarity via an "exclusion" method, by which any brain activity that is related to memory that is *not* associated with recollection is thereby attributed to familiarity. In fact, this means of defining familiarity has been the standard approach in almost all cognitive neuroscience experiments on recollection and familiarity (as outlined by Paller, Voss, & Boehm, 2007). However, little evidence exists to support the validity of this exclusion approach. We propose that this practice is extremely problematic, because many kinds of neural processing can be related to memory yet are not necessarily associated with familiarity, including implicit processing. The exclusion approach will lump all of this processing into the familiarity category without adequately testing whether it is functionally related to familiarity.

A prime example of the fruit of the exclusion approach is the erroneous link between familiarity and a particular event-related brain potential (ERP) known as the FN400 (also known as the mid-frontal old/new effect; Rugg & Curran, 2007). The FN400 is a negative deflection at approximately 400 ms that is sometimes maximal at frontal electrode locations. Several recognition memory experiments have found that item repetition affects FN400 amplitude independently of experimental manipulations that influence the experience of recollection. By contrast, recollection is typically found to vary in conjunction with other ERPs, particularly the late positive complex (LPC) (see below[1]). Thus, in keeping with the aforementioned exclusion approach, effects on FN400 have been attributed to familiarity. For example, among the most cited pieces of evidence for this attribution is a study that utilized a plurality switch from study to test (e.g., study the word "apple" and be tested on the word "apples," thus requiring memory for the plurality "source"; Curran, 2000), to attempt to dissociate the neural correlates of recollection and familiarity. In that study, both FN400 amplitude and familiarity varied for studied compared to unstudied words, but neither depended on plurality. In contrast, the plurality switch reduced the experience of recollection as well as the LPC. The author therefore concluded that FN400 constitutes a neural correlate of familiarity. However, this is a faulty conclusion, because FN400 could have reflected any memory processing unaffected by the plurality switch and unrelated to recollection—such as implicit memory processing—instead of or in addition to familiarity. The same case can be made for virtually every other experiment putatively linking FN400 to familiarity (as reviewed in Paller et al., 2007). Although the possibility of implicit processing during explicit memory tests (and vice versa) has long been appreciated (Richardson-Klavehn & Bjork, 1988), this possibility is overwhelmingly ignored with regard to the interpretation of relevant neural data. It is especially problematic that implicit memory processing is not measured in studies claiming to separate FN400 correlates of familiarity from implicit memory (e.g., Curran & Doyle, 2011; Jager, Mecklinger, & Kipp, 2006; Woodruff, Hayama, & Rugg, 2006), and therefore these studies do not meet their stated goals of separating neural correlates of familiarity from implicit memory processing. Indeed, even findings of correlations between subjective familiarity strength and FN400 amplitude (e.g., Woodruff et al., 2006) constitute evidence from the exclusion approach, given that implicit and explicit memory, although neurocognitively distinct, are often correlated in strength (Paller et al., 2007), and no measures of implicit memory have been included to validate the putative exclusive link between FN400 and familiarity. Indeed, as reviewed below, testing in circumstances in which implicit memory is decoupled from familiarity abolishes the correlation between FN400 and subjective familiarity strength (Voss & Paller, 2009c), thus showing the relevance of implicit memory for FN400. We therefore believe that the link between FN400 and familiarity has arisen as a direct result of the oversight of implicit memory.

Based on this kind of evidence, FN400 has become widely accepted as a generic neural correlate of familiarity (Rugg & Curran, 2007). This assumption has so thoroughly permeated the field that it has become the norm to infer that familiarity occurs whenever an FN400 effect is observed; that is, to infer the experience of familiarity based only on FN400 without any other direct evidence for familiarity (such as subjective report or behavioral performance). This inference pervades the memory literature as well as experiments on other psychological variables (e.g., Czernochowski, Mecklinger, & Johansson, 2009; Ecker, Arend, Bergstrom, & Zimmer, 2009; Klonek, Tamm, Hofmann, & Jacobs, 2009; Mecklinger, Brunnemann, & Kipp, 2011; Nyhus & Curran, 2009; Opitz & Cornell, 2006; Rosburg, Mecklinger, & Frings, 2011; Speer & Curran, 2007). For instance, Rosburg and

[1] Note that many studies have made overly simplistic interpretations of the LPC as a unique and general correlate of recollection (e.g., Curran & Doyle, 2011); yet, there are other, more nuanced interpretations as well (e.g., Finnigan, Humphreys, Dennis, & Geffen, 2002; Marzi & Figgiano, 2010). Nevertheless, although the methods commonly used to link recollection to LPC potentials (e.g., source memory vs. item memory comparisons) are far superior to the exclusion approach used to link familiarity to FN400, and far less likely to be confounded by implicit memory processing, it is far less common to assume a mutually exclusive relationship between recollection and LPC.

colleagues (2011) identified FN400-like effects when subjects demonstrated a simple decision heuristic known as the "recognition heuristic," and on this sole basis they made the erroneous inference that familiarity is part of the mechanism for this heuristic. Furthermore, familiarity has long been thought to involve particular cognitive qualities, such as relative automaticity and rapid onset relative to recollection (Yonelinas, 2002); these qualities are also often inferred based on FN400 without any independent evidence (e.g., manipulations to show that effects are automatic and not influenced by strategy, intentionality, or other factors). The common assumption is thus that of a one-to-one mapping between FN400 and familiarity. However, as described next, there is direct and incontrovertible evidence against this assumption that renders conclusions regarding familiarity in the aforementioned studies invalid.[2]

The one-to-one mapping between familiarity and FN400 necessary to predicate the inference of familiarity from FN400 requires a unique relationship, whereby (1) variations in FN400 effects are always associated with similar variations in the familiarity experience (and not other experiences), and (2) variations in the familiarity experience are always associated with similar variations in FN400 effects (and not other ERP effects). Neither of these conditions holds, based on very straightforward counterevidence. The experience of familiarity can occur for stimuli of many varieties, including words and nameable pictures as well as novel stimuli, such as geometrical patterns, that have never been seen before the experiment. If familiarity is universally associated with FN400, then effects on FN400 should generalize to all of these stimulus categories. However—as described in more detail in the next section—robust FN400 effects are observed due to repetition of words and nameable pictures (Paller et al., 2007; Rugg & Curran, 2007), but FN400 effects are not observed for many types of novel stimuli (e.g., Voss & Paller, 2009c), even when familiarity is strong (e.g., Danker et al., 2008). Furthermore, changing arbitrary features of stimuli, such as coloration, has no influence on familiarity, yet it influences FN400 (Groh-Bordin, Zimmer, & Ecker, 2006). Therefore, variations in FN400 effects are not always associated with similar variations in familiarity (condition 1). Finally, self-reported feelings of increasing familiarity strength had no relationship to effects on FN400 for geometric patterns (Voss & Paller, 2009c), thus demonstrating that variations in the familiarity experience are not always associated with similar variations in FN400 effects (condition 2). In summary, very straightforward evidence weighs against both of the conditions that would need to be met in order to establish FN400 as a generic indicator of familiarity and to permit inferences of familiarity based on FN400.

Given these considerations, it is reasonable to wonder how progress can be made in accurately identifying neural mechanisms of familiarity, and, more specifically, what relationship FN400 potentials have with the experience of familiarity, if any. We have already reviewed the simple evidence against the notion that FN400 is a direct measure of the familiarity experience in all circumstances. However, the fact remains that FN400 and familiarity often co-occur. Therefore, it is worth considering other possible ways that FN400 could relate to familiarity, such as (1) FN400 is a direct measure of a neurophysiological process that serves as a precursor to familiarity in certain circumstances, or (2) it is a direct measure of a process that often occurs at roughly the same time as familiarity but is not a precursor to familiarity. In the next section, we will review evidence that was obtained in an effort to address this issue, emphasizing results from our laboratories. When reviewing this evidence, it is important to keep in mind the ramifications these different outcomes have for our understanding of familiarity memory as well as for relationships between implicit memory processing and subjective awareness. Outcome (1) would suggest that although FN400 may signal one specific precursor to familiarity, the extent to which this or other precursors contributed to familiarity varies with contextual/situational factors. Outcome (2) would suggest that the FN400 reflects other processes—such as implicit memory processes—that are common during recognition testing, and have been misattributed to familiarity simply because they sometimes occur contemporaneously. Determining how FN400 and familiarity are related is therefore central to better understanding familiarity memory as well as the nature of relationships between memory processing and subjective memory experiences more generally.

## CONCEPTUAL IMPLICIT MEMORY PROCESSING DURING EXPLICIT MEMORY TESTING

To explore the functional significance of FN400, it is first necessary to consider the multiple ways in which memory can be expressed, and how the relevant neurocognitive processing can relate—or not relate—to

[2] There is also a strong argument against over-reliance on reverse inference of cognitive processing from neural signals in general, and for an established set of criteria for making relatively valid reverse inferences (Poldrack, 2006) that have not been met for attempts to infer familiarity from FN400.

subjective memory experience. We take as a starting point the very intuitive notion that various kinds of neurocognitive processes can transpire during a memory test, including those that support expressions of memory for which the test was not designed to capture. In other words, although tests of explicit memory are intended to provide measurements of processes relevant to the experiences of recollection and familiarity, neurocognitive processing unrelated to these experiences can nonetheless occur and can influence neural and/or behavioral outcomes. As previously mentioned, a particularly relevant category of processing is that which supports implicit expressions of memory. *Implicit memory* does not involve subjective experiences of memory retrieval, and is characterized as memory processing that occurs when participants do not realize that their behavior has been influenced by past experience. For instance, in priming tests—which are commonly used to measure item-specific implicit memory—procedures typically include initial presentations of specific items followed by tests in which participants perform ostensibly non-mnemonic tasks on repeated items intermixed with new items. In these tasks, participants generally respond faster or more accurately to repeat items even when they evince no explicit memory for the prior encounters. It has long been acknowledged that the implicit memory processing that supports performance in these priming tests can be operative during tests designed to measure explicit memory, and vice versa, such that tests do not generally provide "process pure" measures of either memory type (e.g., Richardson-Klavehn & Bjork, 1988). Again, this is because repeating items during memory tests can have a multitude of effects on processing (Figure 1), including effects unrelated to the particular behavioral outcome that is measured. Therefore, neural measures obtained during explicit testing need not correspond only to forms of explicit memory such as familiarity or recollection, even if these are the only behavioral measures of memory processing collected during the test. Instead, neural correlates of repetition can reflect forms of processing related to implicit memory. This implicit memory processing may contribute to behavioral performance, but it also may not. Thus, considerable effort is needed to disentangle explicit and implicit memory processing and their neural correlates (see also Voss & Paller, 2008a). Indeed, we have argued—using evidence described below—that familiarity has been erroneously associated with FN400 precisely because it has not been disentangled from implicit memory processing, and, in fact, FN400 actually reflects a pervasive type of implicit memory.

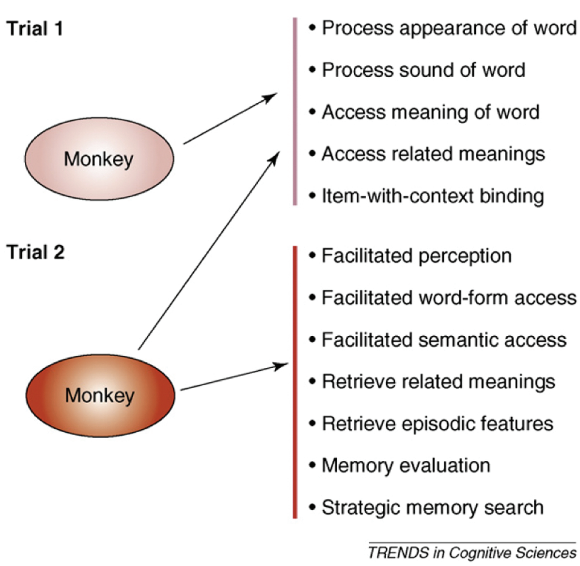


**Figure 1.** Repetition influences many types of neurocognitive processing. Viewing a simple stimulus engages a multitude of neurocognitive processing steps. Likewise, repetition influences many of these same steps and elicits other types of processing as well. Some of these are shown for words and word repetition, highlighting the fact that the processing affected by repetition may or may not be related to the relatively few outcome measures used in a particular memory test. Figure reproduced from Paller et al. (2007) with permission from Elsevier.

Our work in this area was originally motivated by the suggestion by Olichney and colleagues (2000) that N400 repetition effects in explicit memory tests may reflect *conceptual implicit memory*. This suggestion arose because these N400 repetition effects were (1) relatively intact in individuals with impaired explicit memory due to amnesia and (2) similar in several ways to the widely studied N400 correlates of semantic/conceptual processing (Kutas & Federmeier, 2011). Repeating a word, as well as other manipulations that cause facilitated processing of word meaning, causes a positive shift in the amplitude of N400 effects (these positive shifts in amplitude are often called "N400 reductions" in the literature on N400 priming effects, given that the N400 is a negative-going ERP peak that becomes more positive; i.e., it has a reduced negative peak). Word repetition in memory experiments involves a similar positive amplitude shift for FN400, which we argue results because both ERP effects reflect conceptual implicit memory. In the priming literature, conceptual implicit memory involves facilitated processing of conceptual stimulus attributes (e.g., the meaning of a word or object), and is often contrasted with *perceptual implicit memory*, which involves facilitated processing of physical form. Conceptual implicit memory often has been separated from perceptual implicit memory by changing the physical form of a stimulus across repetitions, but not the meaning (e.g., by presenting the same word in different fonts; Schacter, Dobbins, & Schnyer, 2004). The hypothesis that FN400 potentials are related to N400 and reflect concomitant conceptual implicit memory processing during recognition testing, rather than familiarity per se, is of significance for identifying valid relationships between memory expressions and neural processing. Indeed, a demonstrated linkage between FN400 and conceptual implicit memory would imply that implicit memory processing is ubiquitous during explicit memory testing, such that it is operative in virtually all situations in which familiarity for meaningful stimuli has been studied. Conceptual implicit memory thus may be an important but relatively uninvestigated part of the neurocognitive basis of memory.

Our first direct investigations in this area sought to use behavioral measures of both conceptual implicit memory and of the experience of familiarity to disentangle relevant neural processing during a single memory test (as opposed, for instance, to making comparisons based on results from different test formats). Famous faces studied with relevant biographical information, a source of relevant conceptual information that could influence later conceptual priming, were later identified faster than famous faces studied without this information (Voss & Paller, 2006). This conceptual priming provided a behavioral measure of conceptual implicit memory processing during ERP recording. Later, subjects categorized the same famous faces using ratings of the experience of familiarity. Neural correlates of repetition recorded in response to famous faces during the test for conceptual priming were sorted according to their association with conceptual priming (studied with vs. without information) and their association with familiarity (high vs. low familiarity ratings). A “double dissociation” of neural correlates of conceptual priming and familiarity was thus identified: the magnitude of FN400 potentials was associated with conceptual priming but not familiarity, whereas the magnitude of ERP effects occurring after FN400 and with a posterior distribution—the LPC (see Voss & Paller, 2008b)—was associated with familiarity but not with conceptual priming. Furthermore, individual differences in conceptual priming magnitude were strongly correlated with individual differences in FN400, whereby subjects with stronger conceptual priming effects also displayed larger FN400 effects. These individual differences in conceptual priming were not related to LPC amplitude. In contrast, individual differences in familiarity were associated with LPC amplitude, but not with FN400. Notably, these selective associations between FN400 and conceptual priming were identified for a subset of stimuli with familiarity held constant (i.e., all given one familiarity rating level), whereas selective associations between LPC and familiarity were identified with conceptual priming held constant (i.e., just for faces primed with biographical information). These results provide compelling evidence that conceptual implicit memory measured during a priming test is associated with FN400, whereas familiarity in the same circumstances is associated with a distinct ERP correlate (LPC). A follow-up study using similar methods in conjunction with fMRI also found a dissociation between conceptual priming and familiarity (Voss, Reber, Mesulam, Parrish, & Paller, 2008b). Conceptual priming was associated with activity reductions in left inferior frontal cortex, whereas familiarity was associated with activity enhancements in right parietal cortex. These fMRI findings support the link between FN400 and conceptual implicit memory, given that left inferior frontal cortical activity reductions are associated with conceptual priming for a variety of stimulus categories and testing circumstances (Donaldson, Petersen, & Buckner, 2001; Schacter, Wig, & Stevens, 2007). The same comparisons made during the priming test isolated both FN400 and these conceptual-priming-related response reductions, therefore suggesting their linkage and dissociated them from neural correlates of familiarity.

These experiments thus established that conceptual priming and familiarity can co-occur during a priming test, yet produce distinct neural correlates. We next sought to determine whether this pattern extends to recognition memory tests similar to those normally used to associated familiarity with FN400. The primary goal was to identify neural correlates of conceptual implicit memory during recognition memory testing and to compare them to neural correlates of familiarity obtained during the same test. This was a novel comparison, because familiarity and conceptual implicit memory are likely to be correlated under typical recognition testing circumstances (Paller et al., 2007). That is, when words or nameable pictures are used (as is common in recognition studies) familiarity can occur, but so can implicit memory for the conceptual aspects of these meaningful stimuli. To avoid conflating neural correlates of familiarity and conceptual implicit memory, we used stimuli that differed from item to item in their ability to support conceptual implicit memory—yet all stimuli could be recognized with familiarity. Specifically, we determined that novel visual shapes (termed “squiggles” due to their inclusion of curved line segments) evoke meaningful associations in a very idiosyncratic manner. That is, any individual will find meaning only in a subset of squiggles, and there is a high level of variability across individuals with regard to which squiggles are perceived as meaningful. Moreover, this subset is highly consistent for any individual across delays of up to approximately 1 year (Voss & Paller, 2007). Critically, only those squiggles that cue meaningful associations have the capacity to support conceptual implicit memory with repetition. Indeed, meaningful squiggles were found to support conceptual priming in tests involving repeated ratings of meaningfulness, when measured in priming tests, whereas meaningless squiggles were not (Voss, Federmeier, & Paller, 2011; Voss & Paller, 2007; Voss, Schendan, & Paller, 2010). In contrast, both meaningful and meaningless squiggles supported perceptual priming to the same extent in a task involving perceptual judgments, thus indicating a selective association between meaningfulness and conceptual priming. Furthermore, both meaningful and meaningless squiggles can support recognition based on familiarity, and roughly the same proportion of squiggles of the two types yield familiarity responses (Voss et al., 2011; Voss & Paller, 2007). When subjects indicate the experience of familiarity in a recognition memory test, we reasoned that meaningful squiggles would engage neural signals of familiarity plus neural signals of conceptual implicit memory, to the extent that conceptual implicit memory was operative during recognition testing. In contrast, relatively meaningless squiggles would engage neural signals of familiarity, but not of conceptual implicit memory. Therefore, by making comparisons across meaningful and meaningless squiggles that were matched for familiarity, we could isolate neural signals of conceptual implicit memory during recognition testing.

During recognition memory testing, familiarity was approximately matched for meaningful and meaningless squiggles. ERP correlates of familiarity included FN400 and LPC for meaningful squiggles, but only LPC for meaningless squiggles (Voss & Paller, 2007). This pattern of results indicates that FN400 potentials were neural correlates of conceptual implicit memory operative during recognition testing selectively for the meaningful squiggles. Moreover, we also measured conceptual implicit memory during a priming test using the same stimuli, and found that the magnitude of conceptual priming for meaningful squiggles (measured as the repetition-related reduction in response time during the conceptual priming test) correlated with FN400 magnitude (Voss, Schendan, et al., 2010), thereby further supporting the link between FN400 and conceptual implicit memory irrespective of test format. Results from a follow-up study using fMRI also support this conclusion (Voss et al., 2011). Using the same general paradigm, neural correlates of conceptual priming were identified selectively for meaningful squiggles. These correlates included activity reductions in regions of cortex strongly associated with the representation of meaningful objects, such as anterior temporal cortex and anterior fusiform/parahippocampal cortex (Martin, 2007), as well as the same left inferior prefrontal cortex regions generally associated with conceptual priming and identified in our previous experiment that examined priming for famous faces (Voss et al., 2008b). During a recognition memory test, familiarity was associated with activity reductions in the same regions only for meaningful squiggles. In contrast, both meaningful and meaningless squiggles were associated with activity enhancements in prefrontal and parietal cortical regions that are commonly associated with explicit memory and that have been dissociated from conceptual priming (e.g., Donaldson et al., 2001).

To summarize these experiments, neural correlates of conceptual implicit memory for meaningful squiggles included FN400 potentials as well as canonical fMRI correlates of conceptual priming. During recognition memory tests for these stimuli, FN400 and fMRI activity reductions associated with conceptual priming occurred when subjects made familiarity responses, but only for the meaningful squiggles which are also capable of supporting conceptual priming. Although meaningless squiggles were endorsed with familiarity with similar prevalence, the neural correlates of familiarity for these items did not include FN400 or fMRI activity reductions in the same regions. In contrast, familiarity for both meaningful and meaningless squiggles was associated with LPC potentials and fMRI activity enhancements in the explicit retrieval network. We can therefore conclude that meaningfulness can be used to dissociate behavioral and neural signals of conceptual implicit memory and familiarity (Figure 2). Conceptual implicit memory for squiggles is associated with FN400 and fMRI activity reductions in conceptual processing regions, and can occur for relatively meaningful stimuli both during conceptual priming tests and during recognition memory tests.

We also sought to show that these findings are not specific to squiggles and generalize across stimulus categories. We therefore used a very similar approach with uncommon words. Definitions of these words were generally unknown to subjects. In fact, we excluded any words with known definitions for each individual we tested (an average of about 10% of the words). As with squiggles, the remaining words varied idiosyncratically in meaningfulness across participants (Voss, Lucas, & Paller, 2010). Conceptual implicit

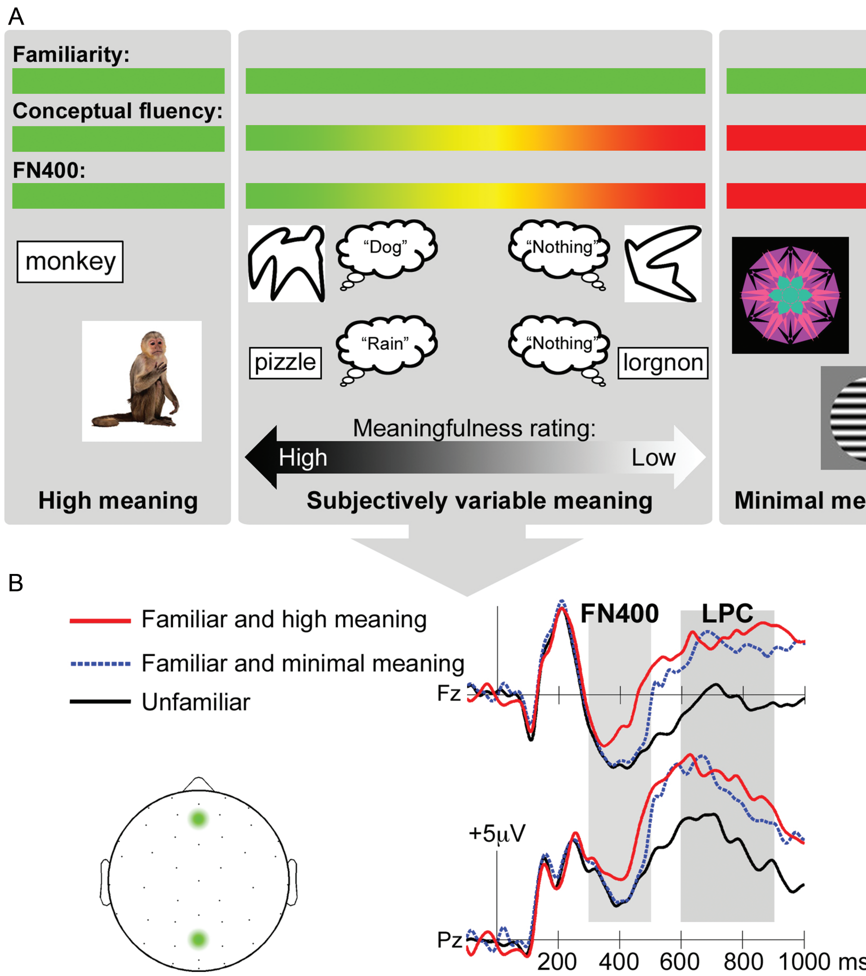


**Figure 2.** Stimulus meaningfulness can be used to dissociate ERP signals of conceptual implicit memory and familiarity. (A) The magnitudes of familiarity, conceptual fluency, and FN400 are shown along a continuum of strong (green) to weak (red) according to variations in stimulus meaningfulness. In repetition paradigms, stimuli that are inherently high in meaning (left) produce familiarity, conceptual fluency, and FN400 (Paller et al., 2007; Rugg & Curran, 2007), whereas stimuli that are minimally meaningful (right) produce familiarity, but not conceptual fluency or FN400 (e.g., Danker et al., 2008; Voss & Paller, 2009c; Yovel & Paller, 2004). Stimuli that vary idiosyncratically across individuals in meaningfulness (middle) support familiarity irrespective of rated meaningfulness, but produce conceptual fluency and FN400 only when rated as relatively meaningful (Voss, Lucas, et al., 2010; Voss & Paller, 2007; Voss, Schendan, et al., 2010). FN400 therefore tracks conceptual fluency rather than familiarity. (B) Example brain potentials are shown for visual words that were matched for familiarity but varied in the degree to which they were thought by the viewer to be meaningful (Voss, Lucas, et al., 2010). FN400 effects (relative to a new-word baseline) were observed only for meaningful words, and FN400 was thus associated with conceptual implicit memory instead of with familiarity. LPC brain potentials were greater than baseline for words endorsed as familiar from both meaningfulness categories and were therefore associated with familiarity.

memory occurred only for meaningful words, as indicated by significant effects in tests of conceptual priming for these words but not for relatively meaningless words. During a recognition memory test, familiarity for meaningful words was associated with FN400 as well as LPC. Familiarity for meaningless words was also associated with LPC, but FN400 was absent (Figure 2B). Therefore, we replicated the findings obtained with squiggles in that conceptual implicit memory was associated with FN400 potentials recorded during a recognition memory test.

Comparisons have also been made between ERP correlates of recognition memory for stimuli of different categories altogether that vary greatly in meaningfulness. For instance, recognition memory paradigms have included items that evoke relatively little in the way of meaningful associations, such as novel faces (Yovel & Paller, 2004; MacKenzie & Donaldson, 2007; but see Donaldson & Curran, 2007), complex and/or novel geometric patterns (De Chastelaine, Friedman, Cycowicz, & Horton, 2009; Voss & Paller, 2009c), and Gabor patches (Danker et al., 2008), and

ERP correlates of familiarity in these circumstances have not included FN400. These images should not be expected to support conceptual implicit memory, and the absence of FN400 is therefore consistent with the link between FN400 and conceptual implicit memory. Nonetheless, this conclusion should be interpreted with caution given that it can be problematic to compare neural correlates across stimulus categories (i.e., common stimuli vs. novel stimuli) and across experiments (i.e., those that examine common stimuli vs. those that examine novel stimuli). However, the selective association of FN400 with meaningfulness was identified in at least one study in which comparisons between common meaningful stimuli and novel, relatively meaningless stimuli were made within the same subjects (Danker et al., 2008). In general, these results therefore reinforce the differences in FN400 based on subjective variations in meaningfulness of squiggles and uncommon words.

Finally, we also recently sought to determine whether FN400 potentials signal conceptual implicit memory for the stimuli most often used in recognition memory experiments: common words (Voss & Federmeier, 2011). Meaningful/meaningless comparisons used in our experiments with squiggles and uncommon words would not adequately capture variations in conceptual implicit memory for common words, given that all common words are relatively high in meaningfulness and would be expected to readily support conceptual priming. Instead, we took a different approach, and used a manipulation of short-term conceptual priming often referred to as “semantic priming.” This method of priming is a standard way to manipulate the N400 correlate of conceptual processing (Kutas & Federmeier, 2011). For instance, N400 amplitude and conceptual processing of the word “doctor” varies according to whether it immediately follows the related word “nurse” or the unrelated word “shoe.” We therefore focused on ERP correlates of familiarity-based recognition for two categories of words: (1) those that were primed by an immediately preceding related word, and (2) those that were not primed (immediately preceded instead by an unrelated word). We reasoned that neural correlates of conceptual priming would be enhanced selectively for the primed words during this recognition test. To the extent that familiarity was similar for these two categories, neural correlates of conceptual priming could therefore be separated from those of familiarity. Subjects made valence judgments (positive/neutral) to each word, followed by a recognition memory judgment using remember, know, guess, and new responses. Consistent with our hypotheses, familiarity-based recognition was nearly identical for primed words and words that were not primed. Familiarity for both word categories was associated with nearly identical FN400 as well as LPC effects (the LPC effects were left-lateralized, as is often the case for recognition memory experiments using words). The conceptual priming manipulation significantly increased the magnitude of FN400 for the primed words, but did not influence familiarity. Therefore, we concluded that conceptual implicit memory was indeed operative during recognition memory testing for words, and was indicated by FN400. Familiarity was also operative—though it was unaffected by semantic priming—and was indexed by LPC. Even when using common words as stimuli, for which familiarity and conceptual implicit memory are often correlated (Figure 2A), these two memory expressions can be disentangled.

Based on these findings from many experiments, we conclude that conceptual implicit memory processing can be indexed by FN400 potentials (at least in the circumstances we have investigated). These potentials appear to selectively associate with conceptual implicit memory during priming tests specifically designed to measure conceptual implicit memory, and also during recognition tests intended to measure explicit memory. Therefore, conceptual implicit memory processing is pervasive during tests intended to measure familiarity and recollection; it is so pervasive, in fact, that its neural correlates have been erroneously assigned to those of familiarity. In many circumstances, especially involving common words and nameable images, familiarity and conceptual implicit memory are correlated. Nonetheless, we have shown that they can be disentangled and linked to distinct neural correlates.

The findings we have summarized thus far suggest that conceptual implicit memory is not a necessary precursor of familiarity. Familiarity and its neural correlates are nearly identical for relatively meaningful and meaningless images, yet conceptual implicit memory and its neural correlates are only present for meaningful images (Figure 2). Furthermore, a priming manipulation that enhanced conceptual implicit memory and its neural correlates did not enhance familiarity or its neural correlates (Voss & Federmeier, 2011). It remains to be seen whether conceptual implicit memory can support or influence familiarity in some circumstances. Indeed, some behavioral evidence suggests that manipulations of conceptual implicit memory can sometimes influence familiarity (see below and Dew & Cabeza, 2011). However, the consistent patterns of dissociation between conceptual implicit memory and familiarity described here suggest that implicit memory is by no means necessary to produce familiarity. Moreover, in the following section, we review evidence that implicit memory processing can drive behavioral responses on explicit memory tests in the absence of recollection or familiarity. These findings thus raise the possibility that what appear to be influences of implicit memory on familiarity can sometimes reflect a direct impact of implicit memory processing on behavioral performance during explicit memory tests, without any need for familiarity to mediate the linkage between implicit memory processing and behavior (just as implicit memory influences behavior during priming tests, without any necessary explicit feelings of familiarity).

## EXPLICIT MEMORY IN NAME, IMPLICIT MEMORY IN NATURE

The preceding section presented arguments supporting the notion that neural signals during explicit memory tests can sometimes reflect implicit memory processing. This notion calls into question the assumption that the neural measures one observes are necessarily linked to behavioral and/or subjective qualities of memory that are expressed at the same time. We will now review another set of findings that demonstrates an even stronger way in which memory tests are not "process pure." In these experiments, behavioral expressions of memory during tests intended to measure explicit memory do not reflect explicit memory at all, but instead are determined by implicit memory processing. These results demonstrate the ability of implicit memory processes to guide behavioral choices during memory testing—not because they interact with explicit memory, but because they can direct mnemonic behaviors without involving the sense of awareness that characterizes explicit memory.

It is commonly assumed that performance in recognition memory tests reflects explicit memory processing, partly because confident recognition responses can be dissociated from implicit memory processing (e.g., Conroy, Hopkins, & Squire, 2005; Stark & Squire, 2000; Wagner, Gabrieli, & Verfaellie, 1997). However, there is also evidence that responses during recognition testing can be influenced by implicit memory, such as when increases in perceptual and conceptual fluency cause an increased tendency to endorse fluent items as studied (e.g., Keane, Orlando, & Verfaellie, 2006; Verfaellie & Cermak, 1999; Whittlesea & Williams, 2000; Wolk et al., 2005). Some findings suggest that this influence is particularly strong for familiarity responses (e.g., Rajaram & Geraci, 2000), consistent with the notion that the experience of familiarity can arise when the sensation of fluency is attributed to prior experience (Whittlesea & Williams, 2000). However, an alternative possibility is that influences of implicit memory on recognition responses are not accompanied by the phenomenology of familiarity or of any conscious memory experience. In other words, it could be that a false link has been made between implicit memory and familiarity merely because individuals in most of these memory experiments do not have the choice to respond "guess," but can only respond with "recollection," "familiarity," or "new" (or just "old" or "new"). In this way, the link between these behavioral responses and the experience of familiarity is inferred based on the widespread assumption that performance in these tests reflects only explicit memory phenomena. Indeed, in one experiment individuals were given the option to respond "guess"—signaling no subjective experience of memory retrieval—in addition to the standard recollection and familiarity options (Tunney & Fernie, 2007), and the relationships between test cue fluency and memory responses were measured. Fluency effects in this experiment were restricted to guess responses, and did not influence familiarity. This demonstration suggests that implicit memory processing may not necessarily lead to an increased sense of familiarity, and that experimenters have potentially identified false associations between fluency and familiarity because "guess" or "no awareness" response options were absent. Instead, implicit memory processing may directly drive behavior during recognition testing, influencing accuracy without simultaneously engendering any subjective memory experience.

To test these ideas, we assessed recognition memory for complex geometrical patterns ("kaleidoscope images") in order to limit the subject's ability to invoke semantic/conceptual encoding or elaborative retrieval strategies that promote explicit memory (Figure 3A). Indeed, we found that subjects rarely find these stimuli to be meaningful, endorsing less than 8% of images as being meaningful whatsoever, with an average rating value corresponding to "no meaning whatsoever," when the sole task was to attempt to find meaning in the images (Voss & Paller, 2009c). We also developed recognition test parameters intended to either increase or decrease the relevance of implicit memory processing for accurate responding. These parameters allowed us to determine whether influences of implicit memory on recognition engender subjective experiences of familiarity, or, conversely, occur without awareness of these influences. Divided attention during encoding has been found to reduce subsequent explicit memory without affecting subsequent perceptual implicit memory (Mulligan, 1998). We therefore used

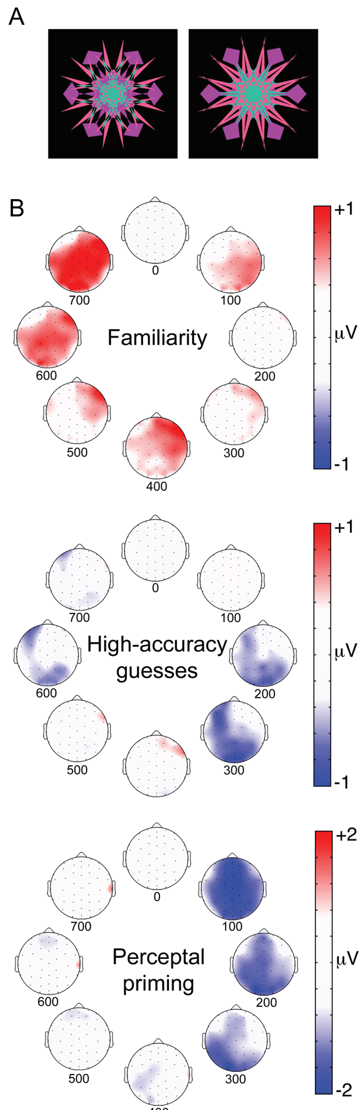


**Figure 3.** Distinct neural signals of recognition based on familiarity versus perceptual implicit memory. (A) An example target/foil pair of kaleidoscope images is shown. One image from the pair was studied, and later presented alongside its matched foil during forced-choice recognition testing. (B) ERP signals of three distinct expressions of memory for kaleidoscope images, including (1) recognition based on familiarity, (2) recognition based on highly accurate guess responses without any awareness of memory retrieval, and (3) enhanced identification speed and accuracy indicative of perceptual priming (Voss & Paller, 2009a, 2010a). Our interpretation that highly accurate guess responses during forced-choice recognition testing were based on perceptual implicit memory is supported by the striking similarities between ERP correlates of accurate guesses and ERP correlates of perceptual priming. Notably, ERP correlates of familiarity were distinct from both ERP correlates of highly accurate guessing and ERP correlates of perceptual priming. Panel B adopted from Voss & Paller (2010b) with permission from Cold Spring Harbor Laboratory Press.

both full-attention and divided-attention encoding conditions in order to manipulate the ability of subjects to engage in study operations that support explicit memory. In addition, we alternately used either a yes/no format for testing recognition or a forced-choice format, wherein each target that was repeated from the study session was presented alongside an unstudied foil with a very similar appearance (Figure 3A). The latter format was intended to enhance the ability to use differences in visual fluency between the target and the foil as a signal for old/new discrimination. Even though some targets would be more fluent than others, each target would tend to be more fluent than its corresponding foil. Indeed, it has long been appreciated that perceptual discrimination can be performed without awareness only for highly similar stimuli during forced-choice format tests (Adams, 1957), because gross perceptual stimulus differences enhance the role of awareness in discrimination.

In several experiments, we identified striking influences of implicit memory on recognition performance when the aforementioned testing parameters encouraged a reliance on fluency (Vargas, Voss, & Paller, 2012; Voss, Baym, & Paller, 2008a; Voss & Paller, 2009a, 2010b). Furthermore, these influences occurred without awareness of retrieval on the part of subjects. We instructed subjects that "guess" responses were to be made during tests only when recognition responses were unaccompanied by awareness of retrieval—that is, when the subjects were blindly guessing. Nonetheless, on the forced-choice tests, these guesses were highly accurate. In fact, they were significantly more accurate than were familiarity responses accompanied by awareness of retrieval (Voss & Paller, 2009a, 2010b). In contrast, guess response accuracy during yes-no format tests was no better than chance (Voss et al., 2008a). Because forced-choice guess responses were devoid of any experience of explicit memory, including recollection and familiarity, we reasoned that highly accurate guesses were based on implicit memory for the perceptual attributes that allowed fluency-based discrimination of targets from foils selectively during forced-choice testing.

Several findings support this implicit-memory account of accurate guess responding:

1. Performance in all experiments that used forced-choice testing increased when study was performed with divided attention as opposed to full attention. This pattern is opposite to the deleterious effects that dividing attention during encoding commonly has on explicit expressions of memory (Mulligan, 1998). In contrast, yes-no performance showed the standard effect of reduced accuracy with divided attention. Furthermore, guesses were highly accurate for both full- and divided-attention encoding.

Subjects were instructed to memorize kaleidoscope images for the upcoming tests, and attention was divided by having subjects perform a concomitant 1-back task using auditory numeric digits, involving an odd/even judgment during trial $n$ for the digit from trial $n - 1$. Divided-attention encoding reduced the prevalence of explicit memory responding, and yet increased overall accuracy by making highly accurate guesses more prevalent. Therefore, when explicit memory was reduced by divided attention during encoding, guess responses based on intact perceptual implicit memory exerted greater influences on overall performance.[3]

2. This divided-attention advantage on forced-choice format tests was eliminated when gross perceptual differences were introduced between targets and foils, therefore presumably limiting the relevance of implicit fluency signals (Voss et al., 2008a; see also Migo, Montaldi, Norman, Quamme, & Mayes, 2009).
3. The divided-attention advantage on forced-choice tests was also eliminated when subjects were given an extended period of time to respond during the test (Voss et al., 2008a), as this presumably encouraged deliberation and explicit-memory-based responding.
4. Likewise, the high accuracy of guess responses was eliminated when subjects were encouraged to adopt an explicit retrieval strategy, whereas guess responses remained highly accurate when subjects were encouraged to respond without attempting explicit retrieval (Voss & Paller, 2010b; see also Jeneson, Kirwan, & Squire, 2010, for a similar trade-off between prevalent explicit memory responding and guess accuracy).

Based on these findings, we concluded that our testing parameters were suitable for identifying influences of implicit memory processing on a recognition test of the variety commonly assumed to measure only explicit memory. Furthermore, when implicit memory influenced performance, this influence was limited to guess responses that conveyed a lack of retrieval awareness. Experiments on implicit recognition collectively indicate that highly accurate guesses during recognition testing are most prevalent when (1) subjects follow instructions to minimize explicit memory strategies and make many guess responses, (2) manipulations at study such as rTMS or divided attention are used to reduce strategies that aid explicit memory, (3) the test format emphasizes perceptual information by utilizing a forced-choice format, and (4) responses are made without much deliberation during test (based on either response deadlines or instructions to guess freely).

The neural signals related to highly accurate guesses lend additional support to the interpretation that these responses are based on perceptual implicit memory. Highly accurate guesses were associated with greater ERP negativity for targets compared to foils at occipital and left frontal recording sites from approximately 200–400 ms after stimulus onset (target and foil ERPs were separated by an alternating-presentation forced-choice design that produced the same behavioral effects as the original behavioral experiments). In contrast, both recollection and familiarity were associated with greater ERP positivity at distinct locations and latency intervals (Voss & Paller, 2009a). Furthermore, a negative fronto-occipital effect similar to that identified for accurate guesses was also related to behavioral measures of perceptual implicit memory for the same kaleidoscope images in another experiment. Perceptual implicit memory was identified as faster and more accurate responding for repeated compared to new kaleidoscope images during a priming test involving perceptual judgments of color composition, and the magnitude of these negative fronto-occipital ERPs scaled with response speed such that greater magnitude related to faster responding (Voss & Paller, 2010a). Thus, ERP effects associated with perceptual implicit memory during a priming test were similar to those identified when subjects made highly accurate guess responses during forced-choice recognition testing (Figure 3B).

Fronto-occipital negative ERP effects similar to those we have found in association with highly accurate guess responses have also been linked to implicit memory and have been dissociated from ERP correlates of explicit memory in other experimental circumstances (e.g., Paller, Hutson, Miller, & Boehm, 2003). Notably, these negative repetition effects could be caused by reduced neural responses in frontal and occipital cortex, which have been associated with

[3] Note that we do not propose any necessary role for divided attention encoding in producing these effects. This manipulation is merely one of many that can be used to reduce explicit memory. Indeed, recent evidence shows that similar effects can be obtained using repetitive transcranial magnetic stimulation (rTMS) to disrupt left prefrontal cortical regions important for effortful encoding operations that promote explicit memory. Temporary prefrontal disruption using rTMS just before encoding was associated with significantly enhanced accuracy of guess responses during forced-choice format tests (Lee, Blumenfeld, & D'Esposito, 2011). Without rTMS, guess responses were no better than chance, whereas guess responses after rTMS were significantly more accurate than chance and approximately as accurate as in our experiments.

repetition-related perceptual processing fluency (Schacter et al., 2007). Indeed, recent behavioral findings from our laboratory support the notion that the ERP correlates of implicit recognition partly reflect fluent processing in visual cortical regions. Using a lateralized presentation paradigm, we found that the accuracy of guess responses was significantly influenced by consistency of visual hemifield from study to test (Vargas et al., in press). Whereas guess responses during forced-choice testing for kaleidoscopes presented in the same visual hemifield at study and at test were highly accurate, the accuracy of guess responses for kaleidoscopes presented in different visual hemifields at study and at test was no better than chance. One interpretation of these findings is that highly accurate guesses under these circumstances depend on processing in contralaterally organized visual cortical regions, although additional evidence (e.g., complementary lateralized neural repetition effects) is needed to rule out alternative possibilities. Nonetheless, these findings show that study-test perceptual overlap is an important factor in highly accurate guess responses, thus further implicating the role of perceptual fluency.

Based on these multiple behavioral and neural findings, we conclude that implicit memory processing of perceptual stimulus attributes can have powerful influences on performance in what are ostensibly tests of explicit memory. Furthermore, this implicit memory processing can have a direct influence on performance. In other words, implicit memory processing need not influence performance via an indirect influence on familiarity or recollection. Indeed, only guess responses indicating no awareness of memory retrieval demonstrate effects consistent with implicit memory processing. Furthermore, these guess responses can be dissociated from explicit memory responses, including familiarity, on behavioral and neural grounds. Whereas familiarity responses are less accurate than recollection responses, guess responses can be more accurate than familiarity responses, and of similar accuracy to recollection responses (Voss & Paller, 2009a, 2010b). This U-shaped function across recognition confidence levels is not consistent with the alternative interpretation that guess responses merely reflect weak familiarity and/or weak recollection. Furthermore, neural correlates of highly accurate guess responses were strikingly dissociable from neural correlates of both recollection and familiarity (Voss & Paller, 2009a), and instead resembled neural correlates of implicit memory in a priming test (Voss & Paller, 2010a). We thus conclude that behavioral responses during a recognition test can be directly sensitive to perceptual implicit memory processing, without any necessary role for awareness of memory retrieval. The coupling of behavior to neural signals of memory therefore does not appear to depend on any attributional process involving awareness, just as is the case for most priming tests of implicit memory in which subjects demonstrate faster or more accurate responses without acknowledging any influence (including attributions) stemming from prior experiences.

Note that highly specialized testing circumstances were needed in order to identify these strong influences of implicit memory on recognition performance. It is therefore important to consider whether responses are similarly influenced by implicit memory processing in circumstances more characteristic of explicit memory testing. Although we do not currently know the answer to this question, some considerations suggest a possible role for more general influences of implicit memory processing on recognition performance. Although confidence and accuracy are usually correlated during recognition testing, with high confidence associated with high accuracy and low confidence with low accuracy (Heathcote, 2003; Yonelinas, 2001), this correlation is not universal. It is therefore possible that performance is influenced by implicit memory processing on at least a subset of trials, perhaps especially those involving minimal explicit memory. Furthermore, the association between confidence and accuracy is sometimes inverted, with higher confidence associated with lower accuracy and lower confidence associated with higher accuracy (Dobbins, Kroll, & Liu, 1998; Heathcote, Bora, & Freeman, 2010; Heathcote, Freeman, Etherington, Tonkin, & Bora, 2009; Tulving, 1981). These confidence–accuracy inversions are consistent with the effects we note of highly accurate guesses, as there is a fundamental decoupling of performance and awareness in either case. Notably, all reported confidence–accuracy inversions have been identified by forced-choice format tests with stimuli of relatively high target/foil perceptual similarity. These testing parameters are perhaps generally ideal for enhancing influences of implicit memory processing on recognition performance, suggesting that performance could be driven to some extent by implicit memory pervasively in tests intended to measure explicit memory whenever some of these parameters are included (e.g., in forced-choice recognition tests, including delayed match-to-sample or nonmatch-to-sample tests, and perhaps whenever explicit memory is relatively weak).

## CONCLUSIONS

We hope that our descriptions of the pervasive operation of implicit memory processing will contribute to better mechanistic understanding of both implicit and explicit memory. In our view, aspects of memory processing associated with subjective awareness have been overemphasized, at the expense of accurate descriptions of these mechanisms. The findings we review here underscore why it is important not to prematurely assume relationships between neural measures and self-reported subjective memory states. Experiences such as familiarity often occur at the same time as implicit memory processing, and only by teasing apart these separate processes can relevant mechanisms be identified. Furthermore, it is just as important to refrain from assuming that tests intended to measure explicit memory necessarily do so, as overall performance can reflect combinations of both explicit and implicit memory processing. Premature assumptions based on an overemphasis on self-reported memory experiences have already generated considerable confusion in the memory literature (e.g., with respect to familiarity memory and implicit memory, as reviewed here, and with respect to the development of animal models of explicit memory, as suggested by Voss & Paller, 2009b). The reach of these missteps is being amplified as memory paradigms become increasingly important for mechanistic descriptions of more general psychological functions (e.g., Rosburg et al., 2011, as described above).

It is therefore important that future investigations of memory processing refrain from drawing over-general conclusions solely on the basis of neural correlates, subjective reports, or assumptions about what kind of memory processing contributes to performance in a specific test. Instead, all of these phenomena—neural measures, subjective report, and behavioral performance—should be better integrated in memory experiments (see also Paller, Voss, & Westerberg, 2009, for related suggestions). In the experiments reviewed here, for example, careful assessments of results from self-reports of memory experiences, performance in recognition and priming tests, and neural measures obtained in relation to all of these factors were necessary to disentangle familiarity and conceptual implicit memory and to demonstrate separate influences of explicit and implicit memory processing during recognition tests. In this way, we identified clear distinctions between implicit and explicit memory. Conceptual implicit memory occurred contemporaneously with familiarity, but was not a necessary precursor to familiarity experiences. Furthermore, perceptual implicit memory sometimes determined responding during recognition testing, but without any awareness of memory retrieval or contribution from explicit memory. Implicit memory and explicit memory are co-active in many circumstances, yet can be distinguished by their distinct neural mechanisms considered in conjunction with their unique behavioral ramifications and subjective qualities. Performance and subjective experiences during any given test of memory likely involve a complex interplay of both implicit and explicit memory processing. Overall, our results are consistent with a fundamental dissociation of implicit and explicit memory processing, and show that implicit neurocognitive processing plays vital roles in memory, despite the fact that it occurs without a feeling.

# Commentaries

## Intermixing forms of memory processing within the functional organization of the medial temporal lobe memory system

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**Abstract:** Voss et al. discuss evidence indicating an intermixing of implicit and explicit memory processing, and of familiarity and recollection, in tests of memory. Here I support this view, and add that the anatomy of cortical-medial temporal lobe pathways indicates a hierarchical and bidirectional functional organization of memory in which implicit memory processing contributes to familiarity, and implicit memory and familiarity processing inherently contribute to recollection. Rather than look for new ways to separate these processes, it may be as important to understand how they are integrated.

Voss and colleagues are to be applauded for raising serious discussion about the relationships between multiple dichotomies in memory, explicit vs. implicit memory, recollection vs. familiarity, perceptual vs. conceptual priming, and questioning whether formal behavioral and electrophysiological assays support these distinctions or instead indicate overlap among them. Their review, focused on ERPs as the metric of memory processing, favors the latter and the authors conclude that measures of explicit memory also capture implicit processing and other aspects of overlap.

Many studies have shown the combined contributions of implicit and explicit processing, as well as familiarity and recollection, of the same material. For example, recent work has revealed implicit memory through eye movement patterns as subjects scan novel, familiar, and altered pictures, independent of, but intermixed with, explicit recall (Ryan, Althoff, Whitlow, & Cohen, 2000; Hannula & Ranganath, 2009). Similarly, recent studies in animals have shown that recollection-like and familiarity-like processes contribute in concert to object recognition (Eichenbaum, Fortin, Sauvage, Robitsek, & Favorik, 2010). The question Voss et al. raise is whether the combined contributions of implicit/explicit or familiarity/recollection occur in parallel or interact.

The answer, I suggest, lies in a consideration of the anatomical basis for contributions of various forms of memory processing. The medial temporal lobe memory system involves three stages of interconnected structures: (1) Multiple higher-order single modality and multimodal cortical areas sending outputs that converge on (2) The parahippocampal cortical areas, including perirhinal, parahippocampal and entorhinal cortex, and outputs of these areas project to (3) Subdivisions of the hippocampus; note that major outputs of the hippocampus are sent back to the parahippocampal region and thence back to cortical areas that were the origins of medial temporal input (Eichenbaum et al., 2007; see Figure 1).

There is substantial evidence that perceptual priming is supported by reactivation of modality-specific sensory representations in single modality cortical areas, whereas conceptual priming is supported by reactivation of material-specific multimodal areas (e.g., Keane, Gabriele, Fennema, Growdon, & Corkin, 1991). There is also substantial evidence that perirhinal cortex supports familiarity whereas the hippocampus is critical to recollection (Eichenbaum, Yonelinas, & Ranganath, 2007). Surely, these areas do not support these functions in isolation, but bidirectional interactions between successive stages in this system are required.

Given this organization, it should be clear that distinct types of processing interact in a hierarchical and interactive fashion. The regeneration of modality-specific sensory representations reflected in perceptual priming contributes to the retrieval of more abstract and multimodal representations reflected in conceptual priming. Both of these implicit forms of memory are the main inputs to the medial temporal lobe structures. Thus, implicit memories are the substance of information processing by parahippocampal areas, including perirhinal cortex. Also, familiarity likely arises from bidirectional interactions between perirhinal cortex and appropriate higher-order cortical areas, and thereby intermixes implicit and explicit processing of memories (e.g., a familiar face). Then the outcome of memory processing in perirhinal cortex, as well as other parahippocampal areas, are the substance of information processing within the hippocampus, which relates

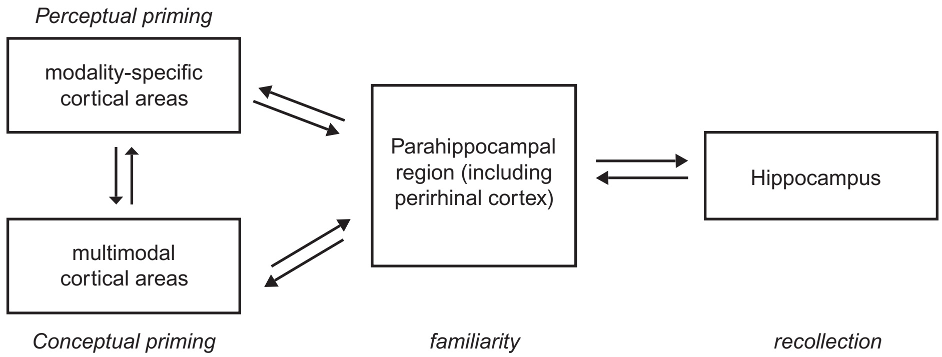


**Figure 1.** An anatomically based model of cortical-medial temporal functional organization.

memories with each other and with the context in which they occur (Eichenbaum, 2004). Thus, recollection arises from bidirectional interactions between the hippocampus and parahippocampal areas, and perhaps throughout the entire cortical-hippocampal system.

From this perspective, the hierarchical organization and two-way interactions within the system are fully expected to intermix the contributions of several forms of implicit and explicit processing within everyday memory as well as formal tests of memory. So, in addition to studying the distinctions between these forms of memory processing, it may be as useful or more useful to examine further how they are integrated.

* * *

# You can feel it all over: Many signals potentially contribute to feelings of familiarity

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**Abstract**: Voss, Lucas, and Paller provide a thought-provoking summary of their recent research showing that neural effects which are often attributed to (explicit) feelings of familiarity can instead be attributed to the (implicit) effects of conceptual priming. Here, we discuss research that shows effects of priming on (putative) behavioral and neural measures of familiarity, and consider a slightly different interpretation: That multiple neurocognitive processes can serve as signals to prior experience with a test item (i.e., can influence judgments of familiarity), and the set of signals that will be interpreted as familiarity depends on the experimental context.

Voss et al. review recent research showing that behavioral and neural effects that are typically attributed to "familiarity", an explicit memory judgment, can instead be attributed to conceptual priming, an example of implicit memory. We are sympathetic to the view that the influence of implicit memory on direct tests of memory is often underestimated, particularly in relation to concurrent neuroimaging data. To underscore this point, we discuss some research that uses masked primes to influence the processing fluency of test cues in a recognition memory paradigm. Our interpretation of these effects differs in detail, if not in spirit, from that proposed by Voss et al.

As Voss et al. note, previous exposure to an item increases fluency of processing on subsequent encounters with the same item—a classic implicit memory effect. Although this increase in fluency due to prior exposure can influence participants' performance without their awareness, such fluency could also contribute to feelings of familiarity and hence influence explicit memory judgments. Jacoby and Whitehouse (1989) found evidence for just this sort of effect: Repetition primes presented briefly immediately before recognition-memory test items increased the likelihood that participants would judge those items as "old". The increased tendency to judge primed items as "old" occurred even for items that had not been previously

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studied, suggesting that processing fluency was being (mis)attributed to memory. Subsequent studies have found that this fluency manipulation selectively increases "Know" and not "Remember" responses, suggesting that fluency is interpreted as familiarity (Rajaram, 1993; Woollams, Taylor, Karayanidis, & Henson, 2008).

The finding that processing fluency can influence familiarity underscores Voss et al.'s warning that the contribution of implicit memory processes must be considered before conclusions about putative measures of explicit memory are drawn. However, not all such measures of explicit memory can be entirely explained by priming: In an ERP version of the Jacoby-Whitehouse paradigm, we found that effects of priming and of familiarity occurred in the same time-window (300–500ms), but had different topographical distributions over sensors, indicating that their neural sources were not identical (Woollams et al., 2008). This dissociation between ERP effects of repetition priming and of familiarity is perhaps unsurprising since, as Voss et al. point out, familiarity is a catch-all category, operationally defined as recognition without retrieval of context. Prior exposure to an item might increase fluency at any level of processing—perceptual, lexical, conceptual, etc.—each subserved by different neural sources (which may be difficult to distinguish with EEG), and each with the potential to serve as a valid signal of familiarity (e.g., conceptual priming has also been claimed to increase familiarity, Rajaram & Geraci, 2000; though see Taylor, Buratto, & Henson, submitted). The short stimulus onset asynchrony (SOA) masked repetition priming used by Woollams et al. likely emphasized perceptual fluency, which may have only been one of multiple neural signals that contributed to familiarity.

A second likely source of differences between ERP effects of priming and familiarity is the fluency-attribution heuristic itself, or in Voss et al.'s terms, the mechanism by which the memory *process* comes to be interpreted as a memory *experience*. This attribution mechanism appears to be under conscious control: Participants are able to discount fluency arising from obvious non-mnemonic sources, such as when repetition primes are clearly visible, resulting in a reversal of the effect of priming on memory (Jacoby & Whitehouse, 1989). Indeed, whether and how any one type of fluency is used as a memory signal may depend on the broader experimental context, such as the type of information emphasized by the explicit memory instructions (retrieval orientation), or the presence of other sources of fluency. For example, masked conceptual primes increase correct "remember" responses, but only when repetition primes are also present in the experiment (Taylor & Henson, in press).

In summary, we agree with Voss et al.'s general position that a closer look at the memory *experience* of familiarity can reveal the action of underlying implicit memory *processing*. Evidence from a recognition memory paradigm in which test-cue processing fluency is manipulated by priming suggests that fluency at multiple levels of processing can signal that an item has been encountered previously. Future work is needed to identify the circumstances that determine which set of fluency signals will be attributed to memory in any given experimental context.

* * *

## On the contribution of unconscious processes to recognition memory

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**Abstract**: Voss et al. review work showing unconscious contributions to recognition memory. An electrophysiological effect, the N300, appears to signify an unconscious recognition process. Whether such unconscious recognition requires highly specific experimental circumstances or can occur in typical types of recognition testing situations has remained a question. The fact that the N300 has also been shown to be the sole electrophysiological correlate of the recognition-without-identification effect that occurs with visual word fragments suggests that unconscious processes may contribute to a wider range of recognition testing situations than those originally investigated by Voss and colleagues. Some implications of this possibility are discussed.

Voss, Lucas and Paller review work showing unconscious contributions to recognition memory (e.g., Voss & Paller, 2009a). As they note, the circumstances under which such unconscious influences were previously shown were highly specific; these include minimizing reliance on explicit memory, emphasizing relative perceptual information with forced-choice testing, and utilizing guess responses. The authors suggest that whether such unconscious influences play a role in more standard recognition memory tasks remains to be determined.

Recent research suggests that such unconscious processes may, in fact, contribute on tasks that more closely approximate standard recognition testing situations. Ryals, Yadon, Nomi and Cleary (2011) examined the event-related potential (ERP) correlates of the recognition-without-identification effect, which is the finding that when subjects cannot identify the items about which they are being questioned at test, they can still discriminate between those that were studied and those that were not (e.g., Cleary, 2006; Cleary & Greene, 2000; Cleary, Langley & Seiler, 2004; Cleary, Winfield & Kostic, 2007). Ryals et al. (2011) examined the ERP correlates of the recognition-without-identification effect found with visual word fragments (e.g., Cleary & Greene, 2000). Subjects studied words and were tested with visual word fragments, half from studied and half from unstudied words. For each test fragment, subjects attempted to identify the word and gave a yes-no judgment indicating whether the word was studied (even if it was unidentified). The only ERP correlate to the recognition-without-identification effect was the type of N300 effect that Voss and Paller (2009) argued signified unconscious recognition. Regarding what this implies about the recognition-without-identification effect, one should be hesitant to use the very reverse inference that Voss et al. caution against. However, Ryals et al. (2011) also found that the N300 old-new difference was only obtained among those subjects who actually showed the behavioral recognition-without-identification effect; subjects who failed to show the behavioral effect showed no ERP old-new differences among unidentified items. This suggests that the N300 effect is indeed related to the behavioral recognition-without-identification effect, and raises the interesting possibility that the recognition-without-identification effect shown with visual word fragments reflects the same type of unconscious processing shown in Voss and Paller's (2009) study. If so, then this would suggest that unconscious contributions can occur in a wider range of recognition memory testing situations than initially shown by Voss and Paller. In Ryals et al.'s (2011) study, yes-no judgments were given on an item-by-item basis at test, the studied stimuli were words encoded under full attention conditions, and the testing instructions did not at all emphasize trying not to rely on explicit memory.

The idea that unconscious processes may contribute to a wider range of recognition memory decisions than those investigated by Voss and Paller (2009) has far-reaching implications. For example, it is common in the recognition literature to assume that source memory indicates the experience of conscious recollection. However, Starns, Hicks, Brown and Martin (2008) demonstrated above-chance source memory in cases where subjects failed to even recognize a test item as old. Moreover, Kurilla and Westerman (2010) showed above-chance source memory for unidentified visual word fragments when the usual recognition-without-identification effect was not even shown; in this case, above-chance source memory occurred both when there was a failure of recognition (i.e., old-new discrimination) and a failure of identification of the test stimuli. Taken together, the findings of Voss and Paller (2009) and of Ryals et al. (2011) suggest the possibility that the above-chance source recognition shown in these studies resulted from unconscious processing. That source memory might sometimes be unconscious is a notion that undermines the assumption, held by many, that above-chance source memory reflects the experience of conscious recollection.

* * *

## Reconsidering the use of "explicit" and "implicit" as terms to describe task requirements

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**Abstract**: Conscious and unconscious expressions of memory—explicit and implicit memory, respectively—may be used to support performance in a given task, even when the

task demands do not ostensibly require one or the other. Work from Voss, Lucas and Paller reveal that just as indirect tasks can capture the influence of explicit memory, direct tasks of memory can capture implicit memory mechanisms. Consequently, tasks cannot be truly labeled as *explicit* or *implicit;* as such labels presuppose, perhaps erroneously, the nature of memory that supports performance.

Philosophers and psychologists have long remarked that there exist unconscious, as well as conscious expressions of memory (c.f. de Biran, 1804/1929), and much research in the past fifty years has been dedicated to comparing and contrasting the two. By necessity, these concepts of memory were initially examined using different techniques; conscious memory was examined using direct enquiry, whereas unconscious memory was inferred through a change in behavior as a result of prior experience. Research suggested that while amnesic patients who had damage to the medial temporal lobe could not explicitly comment on prior learning episodes, they could nevertheless benefit from prior exposure in some situations, and therefore show memory "implicitly" (Schacter, 1987). Consequently, conscious and unconscious expressions of memory were attributed to different *systems*—explicit and implicit memory systems, respectively (Schacter & Tulving, 1994).

It has become common practice for researchers to equate the particular tasks used to investigate explicit and implicit memory systems (e.g., free recall, priming) with the systems themselves. Thus, the notion of explicit and implicit memory, and their distinct underlying neural systems, has given rise to the notion of *explicit and implicit memory tasks.* Such an approach is not only an oversimplification, as any given task is not likely to be process- (or rather, memory-) pure (Ryan & Cohen, 2003), but it can lead to erroneous conclusions regarding the nature of memory and the underlying contributions to cognition and behavior. For instance, performance on associative priming, often described as an *implicit memory task*, has been shown to be contaminated by explicit memory under certain conditions (Hannula and Greene, 2012), complicating interpretations regarding the organization of normal memory and the nature of the impairment in amnesia.

Work that collected behavioral (i.e., eye movement measures) or neural responses in addition to explicit reports showed that on any given trial within the same task, memory may be indexed via behavioral or neural responses with or without concomitant conscious awareness for the stored representations (Ryan et al., 2000; Hannula & Ranganath, 2009). Thus, it cannot be guaranteed that explicit or implicit memory is being solely investigated across all trials, even if the overall task is labeled as such. Even if participants are not directly asked to examine the contents of their memories, they may nevertheless use whatever information is at their disposal in order to successfully complete a given task, including memories for prior learning sessions for which they had conscious access. As a result, the onus is on any researcher who wishes to comment upon the nature of implicit memory to provide evidence that precautions were taken to rule out any vestiges of conscious contribution.

Now, Voss, Lucas, and Paller provide a compelling case for the converse situation: Those who wish to comment solely upon the nature of explicit memory ought to ensure that there is no confounding influence of implicit memory. Their work demonstrates that under certain circumstances, accurate recognition responses in a direct enquiry task, typically ascribed as an explicit memory task, may be driven by memories that are not available for conscious access. Moreover, the underlying neural mechanisms typically attributed to responses of familiarity, and therefore of explicit memory in general, may additionally capture mechanisms underlying implicit memory.

The cautionary tale provided by Voss, Lucas and Paller will hopefully force researchers to reconsider the use of the terms *explicit* and *implicit* to describe tasks when uncertainty exists regarding whether any or all memory representations that are used to support performance are available to conscious access. Instead, research should describe when performance on any given task fundamentally relies on memory representations that are available to conscious awareness, compared to when performance does not require such conscious access. Such a discussion can then truly reveal the nature of memory, its interaction with conscious awareness, and how it may be used to support ongoing cognition and behavior.

* * *

# Familiarity and conceptual implicit memory: Individual differences and neural correlates

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**Abstract**: Voss, Lucas, and Paller point out that explicit recognition tests can be supported by implicit processes, and that conceptual implicit memory may be reflected in ERP correlates of familiarity-based recognition. Here, we argue that an examination of individual differences indicates that familiarity is coupled with conceptual implicit memory across participants, and that fMRI and patient data indicate that the perirhinal cortex is critical for both forms of memory. We suggest that the same process that leads an item to come to mind readily in conceptual implicit tests may also lead the item to seem familiar in explicit recognition tests.

Voss and colleagues propose that memory tasks are not process pure and that explicit recognition judgments can be influenced by implicit memory. We are in agreement on this point and its implications for interpreting studies of implicit and explicit memory. Models claiming that implicit and explicit memory reflect dissociable systems (e.g., Squire, 2004) have been increasingly challenged by evidence that these forms of memory are not entirely distinct, and that both can be supported by the same brain regions (e.g., Dew & Cabeza, 2011). One recent challenge involves parsing the relationship between conceptual implicit memory and familiarity-based recognition. Tests of conceptual implicit memory and familiarity are found to be sensitive to the same behavioral manipulations (for a review, see Yonelinas, 2002), and as Voss and colleagues point out they can be related to similar ERP effects. One interpretation of these results is that explicit tests are contaminated by implicit processes, or conversely that implicit tests are contaminated by explicit processes. However, we suggest another possibility: The same process that leads an item to seem familiar in an explicit recognition test can also lead an item to come to mind readily in a conceptual implicit test.

We have taken two approaches to examine this hypothesis. First, if the two are related, then they should be correlated across individuals. That is, participants who exhibit high conceptual priming scores should also have high familiarity estimates. To test this, we first had participants incidentally encode words by making abstract/concrete judgments. Afterwards, they made recognition confidence judgments in a test containing a mixture of studied and new words. Receiver-operating characteristics were examined to provide estimates of recollection and familiarity (Yonelinas, 1994). In the last phase, participants completed an implicit-free association task in which they were presented with non-studied cue words and asked to produce the first related word that came to mind. Cues were selected to be associated with studied words from the previous tasks and unstudied baselines. Priming was measured as the proportion of studied words generated relative to baseline. Across participants, overall recognition performance was correlated with conceptual implicit memory performance, and this correlation was driven by the fact that familiarity was correlated with conceptual priming, whereas recollection was not (Wang & Yonelinas, in press).

Secondly, if familiarity and conceptual implicit memory rely on the same process, then they may be dependent on the same neural regions. The perirhinal cortex has been implicated in numerous fMRI studies of both familiarity-based recognition (for a review, see Diana, Yonelinas, & Ranganath, 2007) and conceptual implicit memory (e.g., Voss, Hauner, & Paller, 2009). Nonetheless, these correlational studies leave open the question of whether this region plays a necessary role in these forms of memory. However, left perirhinal damage can lead to impairments in familiarity-based recognition (Bowles et al., 2007; Yonelinas et al., 2002), as well as conceptual implicit memory (Wang, Lazzara, Ranganath, Knight, & Yonelinas, 2010). Moreover, the region of maximal lesion overlap in that latter study included the left perirhinal cortex, a region that was found to be related to increased activation during encoding for subsequently primed items in healthy participants (Wang, et al., 2010).

The simplest conclusion to be drawn from these results is that the same process that supports familiarity-based recognition also supports conceptual implicit memory. This does not mean that familiarity and conceptual implicit memory are identical, as previous results have indicated that familiarity can be supported by both perceptual and conceptual factors (for a review, see Yonelinas, 2002). Nor does it mean

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that there are no differences in the brain regions necessary for these two forms of memory (e.g., the response and decision demands of recognition tasks are quite different from those of implicit tasks, see Donaldson, Petersen, & Buckner, 2001). Finally, future work may demonstrate that different subregions within the perirhinal cortex may be differentially involved in familiarity and conceptual implicit memory.

* * *

## "Implicit contamination" extends across multiple methodologies: Implications for fMRI

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**Abstract**: The article "More than a feeling: Pervasive influences of memory without awareness of retrieval" reviews evidence from ERP studies of recognition memory that the FN400 effect typically ascribed to familiarity may index implicit memory that occurs during recognition testing. We find their argument compelling, and contend that this potential "implicit contamination" is not unique to ERP studies. We suggest an analogous problem affecting fMRI studies, focusing particularly on the perirhinal cortex. Resolving this issue is critical for understanding the relationship between memory and the medial temporal lobes.

The memory literature has dedicated considerable attention to the idea of explicit contamination, in which spontaneous memory awareness may complicate both behavioral and neural indices of implicit memory (e.g., Roediger & McDermott, 1993). However, relatively little attention has been paid to the reverse phenomenon, what we might term *implicit contamination*. The article "More than a feeling: Pervasive influences of memory without awareness of retrieval" (Voss, Lucas & Paller) identifies this as a common confound in ERP studies, and reviews evidence that the FN400 effect typically ascribed to familiarity may index implicit memory that occurs during recognition testing. The evidence put forth makes a compelling case that, if we are to understand the electrophysiological basis of memory, ERP studies of recognition memory must measure and control for concurrent implicit memory.

Importantly, we contend that implicit contamination is not unique to ERP studies. Evidence is mounting that an analogous problem affects studies using functional magnetic resonance imaging (fMRI), with particular implications for the perirhinal cortex (PrC). A vast body of research agrees that the PrC makes an important contribution to recognition memory, particularly familiarity memory (Brown & Aggleton, 2001; Eichenbaum, Yonelinas, & Ranganath, 2007; Henson, Cansino, Herron, Robb, & Rugg, 2003). During retrieval, the PrC typically shows repetition suppression, with greater neural activity during novel relative to studied stimuli, or parametric decreases in neural activity with increasing familiarity (e.g., Daselaar, Fleck, & Cabeza, 2006; Gonsalves, Kahn, Curran, Norman, & Wagner, 2005; Montaldi, Spencer, Roberts, & Mayes, 2006). A predominant explanation is that the PrC responds to novel items (Brown & Aggleton, 2001), in turn decreasing activations for repeated items and producing an efficient neural system for learning (Fernandez & Tendolkar, 2006). The link to familiarity memory could thus be supported by this sensitivity to item representations, independently from the contextual detail that underlies recollection (Eichenbaum et al., 2007).

Separately, however, the PrC has been linked with conceptual implicit memory. PrC reductions have been observed during repeated relative to novel semantic decisions (O'Kane, Insler, & Wagner, 2005) and the magnitudes of conceptual priming and PrC reductions have been linked directly (Voss, Hauner, & Paller, 2009). Additionally, encoding-related PrC activity has been shown to predict later conceptual priming (Wang, Lazzara, Ranganath, Knight, & Yonelinas, 2010). These links between PrC and implicit memory raise the question of whether increased fluency associated with re-processing repeated information may be integral to the function of the PrC during familiarity memory. That is, a neural region overwhelmingly interpreted to index item-specific processing could alternatively reflect fluency-based processing that occurs incidentally with item repetition. Fluency could consequently account for cases in which familiarity and conceptual priming respond similarly to the same experimental manipulations (Yonelinas, 2002).

This alternative interpretation of perirhinal function is consistent with the logic put forth by Voss et al., and we argue that fMRI investigations of recognition memory must similarly isolate and identify the potential contribution of fluency. Resolving this issue is critical for clarifying the relationship between memory and the medial temporal lobes.

* * *

## It is time to fill in the gaps left by simple dissociations

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**Abstract**: Our field has been dominated by the quest for dissociations. A number of the dissociations have gotten us far and the implicit/explicit one is an excellent example. It holds in the vast majority of cases and has furthered our understanding of memory considerably. There are now several very interesting exceptions to this basic rule that highlight how systems may interact and how independence is an option or a default, but not a necessity. We should not throw away the fundamental dissociation, but nor should we fail to learn from the interesting exceptions.

Voss, Lucas, and Paller raise a number of excellent points in their paper. While I might take issue with the claim that there has been a "near-exclusive focus on conscious, or explicit expressions of memory" (there is a vast amount of literature that studies implicit forms of memory like categorization, priming, etc.), this is not their central tenet. Their central tenet is that the borders between implicit and explicit memory, interactions between them, and the fact that any task will reflect some mixture of processes has been neglected to our detriment. I agree wholeheartedly with this view.

Studies of severely amnesic patients like H.M. and E.P. have taught us many things as have the studies of rodent and primate animal models of amnesia. One thing they have reliably shown is that implicit and explicit forms of memory can be independent and we can design tasks in which the behavioral outcome is dictated largely, if not entirely, by one form of memory. In my own work, despite trying to push patient E.P. to tap into his intact implicit memory for words, recognition memory remained steadfastly at chance (49.9% correct) across numerous experiments, even when a stem-completion probe immediately preceded the recognition memory probe for each item (Stark & Squire, 2000). That these forms of memory can be independent is a clear contribution to our understanding of memory. However, this does not mean that we should adopt a Fodorian view (Fodor, 1983) of complete modularity as these demonstrations do not show that they must be independent.

Amnesia and its animal models have taught us other things as well. For example, we can see that these various memory processes typically occur in parallel. Even if the behavior is driven largely or entirely by one memory process or system, others will continue to show learning and memory (Packard & McGaugh, 1996). Learning is typically ubiquitous and automatic and comes in many forms. Further, these studies combine with decades of cognitive psychology to show unequivocally that the instructions (and/or task demands) matter a great deal and help push the behavior to be driven by different memory processes or systems. The instructions push—and they bias—but this needn't be an all-or-none process.

Let me use as an example their observation of implicit memory effects on a recognition memory task (e.g., Voss & Paller, 2010). The authors have replicated this effect several times (see the manuscript for review), but it also has a notable replication failure (Jeneson, Kirwan, & Squire, 2010). As noted, a clear legacy of amnesia (and of cognitive psychology) is that we use instructions and task demands as ways of biasing participants to have behavior driven by one form of memory largely over others. Why should it be surprising that there is something about the experiment (instructions, stimuli, context, mood, etc.) that can push subjects to have their behavior driven by implicit memory more than explicit memory despite the more overt task demands? While it certainly appears to be the case that the vast majority of the time when participants perform standard laboratory recognition memory tests, "explicit" memory and the medial temporal lobe are in the driver's seat, why should it be surprising that under specific circumstances this can be over-ridden? Isn't this exactly what the initial reports (and now decades of research) into implicit vs. explicit memory have taught us? Despite external similarities, simply changing the instructions and/or demands can have a huge effect on what memory process or system drives behavior. What exactly is driving their effect (Voss & Paller, 2010)?

Finding out the key factors and boundary conditions will push us forward.

Their data do not overturn or call into question the dissociations in amnesia or the notion that these systems can operate separately if pushed to do so. They don't indicate even that under typical circumstances, implicit memory drives recognition memory performance to a significant degree. These basic ideas are well-established and their findings show us more detail. They show us that while the dissociation captures much, it is not perfect and that there can be exceptions to the rule. Other studies have shown exceptions to the dissociation rule as well. Chun and Phelps' (1999) demonstration of an implicit visual search task relying on medial temporal lobe (MTL) structures (but seemingly not the hippocampus per se; Manns & Squire, 2001) demonstrates this as does the often-used visual paired comparison task (which is implicit in nature but relies upon the MTL).

Our dissociations have taken us far. It is time for us to learn from the interesting cases of how and when the dissociations break down and how and when the many memory processes and systems interact.

* * *

# The impact of fluency on explicit memory tasks in amnesia

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**Abstract**: Distinguishing implicit and explicit memory and delineating their relationship has haunted memory researchers for decades, and Voss et al. provide an impressive overview of their work examining these issues. We briefly comment on the following: (1) There is evidence indicating that implicit memory impacts cued recall, in addition to recognition; (2) Fluency can manifest as priming in implicit memory or it can be experienced as familiarity (in association with attribution processes) in recognition tasks; and (3) The impact of fluency on accuracy of "guess" responses during recognition memory in normal subjects is reminiscent of similar effects on recognition in amnesia.

Voss, Lucas, and Paller (VLP) provide a detailed description of a primary challenge facing memory researchers: Integrating neural data, behavioral performance, and subjective report. Their review motivates consideration of the broader distinction between implicit and explicit memory processes and their relationship. They argue that: (1) Conceptual priming has a distinct neural correlate from familiarity-based recognition; and (2) There is no one-to-one mapping between these two measures. Despite these differences, they emphasize the "accidental capture" of implicit memory in recognition.

Influences of implicit memory on explicit memory performance are not unique to recognition but are also observed in cued recall. In amnesic patients, similar word stem completion performance has been observed under explicit cued recall and "opposition" instructions (to isolate implicit memory, subjects are asked to exclude studied items). This has been taken as evidence that their explicit memory performance is largely based on implicit memory (Cermak, Mather, & Hill, 1997). Similar implicit effects on cued recall have been described in normal cognition (McCabe, Roediger, & Karpicke, 2011).

Unlike VLP, we do not consider this "capture" of implicit memory in explicit memory tasks to be accidental. Rather, we postulate that enhanced fluency (facilitated processing) that manifests as priming in implicit memory can be experienced as familiarity during recognition. Thus, we postulate a more direct link between fluency and feelings of familiarity. VLP might argue against such a view based on the failure to obtain a one-to-one mapping between priming and familiarity, but it is important to consider that whereas priming is a direct consequence of fluent processing, familiarity requires an additional process whereby fluency is attributed to a memorial source.

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Whether fluency is attributed to previous experience will depend on both task and individual factors. When an alternate source of fluency is readily apparent, a feeling of familiarity may not result because there is no discrepancy between the experienced and expected fluency (Whittlesea & Leboe, 2003). Informative in this regard is a comparison of results obtained by Voss and Federmeier (2011) and Rajaram and Geraci (2000), as both examined the effect of semantic priming on recognition. In the former study, which used a long stimulus onset asynchrony (SOA) between semantic prime and target (5.5–7s), conceptual fluency did not affect recognition. By contrast, in the latter study, which used a short SOA (250ms), conceptual fluency did affect recognition. With a long SOA, there was ample time to note the relationship between prime and target, and thus the fluency was expected. With a short SOA, the experienced fluency was higher than expected, and this discrepancy was attributed to familiarity with the target. Familiarity responses are also affected by subjects' willingness to utilize a fluency signal and the criterion set for making familiarity judgments. Manipulating information about the alleged proportion of study items in a recognition test (70% vs. 30%; although in fact the proportion was held constant) improved memory discrimination in amnesic patients, with the enhancement reflecting a selective enhancement of familiarity-based recognition (Verfaellie, Giovanello, & Keane, 2001). Reliance on fluency signals in recognition may also be influenced by the processing approach encouraged by the task (Voss & Paller, 2009a).

An intriguing finding presented by VLP concerns instances in which fluency enhances accuracy of "guess" responses in recognition paradigms. The influence of fluency on guess responses in healthy subjects is reminiscent of similar effects in recognition tasks in amnesic patients. Indeed, the conditions outlined as being conducive to fluency effects are characteristic of amnesia. In the context of normal cognition, when fluency effects translate into the experience of familiarity or simply into guess responses will be an important question for future study. Here as well, attention to factors that influence willingness to engage an attributional process may be useful in understanding the link between fluency and its varied expressions in recognition memory.

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# Electrophysiological correlates of memory processes

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**Abstract**: In this commentary we highlight what are to our minds conflicting findings that have been employed to argue for different functional accounts of the mid-frontal event-related potential (ERP) old/new effect. We also offer our views on the difficulties associated with measuring conceptual priming as well as familiarity, and reemphasise that these issues are only a sub-set of those to consider when assessing the ERP literature that is germane to the question of the processes that the mid-frontal ERP old/new effect indexes.

It is acknowledged widely that the terms used to describe memory tasks should not overlap with those used to describe the processes engaged during completion of the tasks. This distinction emphasizes that implicit as well as explicit memory processes might be active irrespective of whether task instructions in memory studies orient participants to information encoded previously. Voss et al.'s target article is a reminder of this point, with one articulation of their wider argument for the importance of implicit memory research cast in terms of whether the functional significance of an event-related potential (ERP) modulation—the FN400 or mid-frontal ERP old/new effect—is aligned more closely with an explicit memory process (familiarity) or an implicit process (conceptual priming).

Among the data they cover in their target article, Voss and colleagues highlight three of their ERP studies in which measures of conceptual priming as well as measures of explicit memory were available (Voss & Paller, 2006, 2007; Voss, Lucas, & Paller, 2010). In each case, a link between the mid-frontal old/new effect and conceptual priming would stem from variations in the old/new effect alongside variations in priming when familiarity is equated.

In one of these three reports, Voss and Paller acknowledged that their measure of explicit memory cannot isolate familiarity (Voss & Paller, 2006). In the remaining two, visual inspection of the averaged data suggests that familiarity estimates are equivalent while conceptual priming varies only if accompanying differences between estimates of recollection are not considered (Voss & Paller, 2007; Voss, Lucas, & Paller, 2010). Voss et al.'s arguments would be stronger were they to show that familiarity estimates in these studies remain equivalent after concomitant differences between estimates of recollection are controlled for. The data points in their 2010 paper appear to be those for which the claim of statistically equivalent contributions from familiarity while priming varies is most likely to be maintained.

Were this speculation to be correct, then the data would be at odds with those reported by Stenberg and colleagues (Stenberg et al., 2009). In a modified recognition memory task for names, they showed that the mid-frontal old/new effect varied with name frequency but not with whether the names referred to famous or unknown individuals. Estimates of familiarity derived from receiver operating characteristic (ROC) data were coupled with frequency rather than fame, while in a separate assessment of conceptual priming, fame but not frequency promoted priming. Lucas, Voss, & Paller (2010) have already commented on these results, identifying their reservations about the findings as well as additional outcomes that would bolster Stenberg et al.'s claims. In a subsequent response, Stenberg and colleagues reported outcomes that appear to meet at least some of the criteria Lucas et al. set (Stenberg et al., 2010). These appear to us to be data points that merit further discussion.

Convergence on a consensual account for the functional significance of the mid-frontal ERP old/new effect is important. The focus in this brief commentary is on only a subset of the issues that we think merit further consideration, another of note being the marked heterogeneity in analysis strategies across studies where ostensibly the same effect is being analyzed (for a similar comment see Voss & Federmeier, 2011). It is to be hoped that the debate in this Special Issue will result in progress towards identification of data points and perhaps future experiments that have the potential to adjudicate between alternative interpretations.

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# Reply to Commentaries

# On the pervasive influences of implicit memory

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In Voss, Lucas, and Paller (2012) we reviewed evidence that behavioral, neural and subjective phenomena often considered to be hallmarks of explicit memory can be powerfully influenced by processing related to implicit memory. We argued that, as a result, behavioral and neuroimaging experiments designed to measure explicit memory are sometimes prone to capture aspects of implicit memory instead. The nine commentaries published in response to our target article largely resonated with these conclusions. Here we highlight the numerous additional insights offered by these commentaries regarding the circumstances and precise mechanisms that may characterize relationships between implicit and explicit memory, and we describe similarities and differences with our interpretations.

***Keywords:*** Implicit memory; Explicit memory; Recollection; Familiarity; Awareness.

We are fortunate that so many excellent commentaries were written in response to our target article (Voss, Lucas, & Paller, 2012). They largely resonated with our viewpoints and showed how our focus—influences of implicit memory processing on behavioral, neural, and subjective qualities associated with explicit memory—is being pursued by many laboratories and with many approaches. For example, Cleary described how the recognition-without-identification effect studied in her laboratory is similar to the implicit recognition effects we have characterized, and suggested that these phenomena might stem from similar neural mechanisms. Taylor and Henson highlighted fluency effects on recognition behavior and ERPs produced when recognition test cue fluency is manipulated via masked priming. Commentaries by Dew and Cabeza and by Wang and Yonelinas described research on the role of fluency in generating neural responses in perirhinal cortex during recognition testing, while Eichenbaum put forth a well-reasoned neuroanatomical account of possible interactions between implicit and explicit memory processes. These contributions extend the issues raised in our article beyond the specific tasks and measures we described.

Although we emphasized effects on familiarity, commentaries by Hayes and Verfaellie and by Cleary emphasized that implicit memory processing may more broadly influence all manner of explicit memory expression. For instance, implicit memory processing has been shown to influence performance in tasks designed to isolate recollection (Cermak, Mather, & Hill, 1997; McCabe, Roediger, & Karpicke, 2011; Starns, Hicks, Brown, & Martin, 2008; Kurilla and Westerman, 2008). The assumption that subjective experiences of recollection mediate performance on recall and source memory tasks is arguably even more widespread than the assumption that familiarity experiences dictate all recollection-free recognition decisions. That neither assumption is safe strongly bolsters the argument put forth by Ryan that it is problematic to use the terms “implicit” and “explicit” to describe memory tasks—even recall tasks—because these terms presuppose the degree to which conscious awareness mediates task performance.

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Other commentaries provided alternate ways of thinking about relationships between implicit memory processing and explicit memory performance. In particular, some commentaries took issue with the idea that such influences should be described as "accidental" or the product of "contamination." Commentaries by Taylor and Henson, by Wang and Yonelinas, and by Hayes and Verfaellie suggested that these influences instead reflect a common source for implicit and explicit memory expressions. Indeed, the notion that the same fluency signals that produce implicit priming effects can also produce experiences of familiarity on recognition tests is a central tenet of long-standing fluency-attribution accounts of familiarity (e.g., Jacoby & Dallas, 1981; Whittlesea, Jacoby, & Girard, 1990). We entertained this possibility in our target article, and we agree that priming and familiarity may derive from the same fluency signals under some circumstances. As a point of clarification, we used the term "accidental" not to suggest that fluency effects on familiarity are somehow an accident. Rather, we used this term to suggest that experimenters seeking to isolate neural correlates of explicit memory can accidentally measure implicit memory instead, if they fail to take into account that some combination of the two types of processing are engaged in many circumstances. It is no accident that individuals sometimes interpret fluency signals as familiarity; rather, such attributions constitute one way that memory decisions can be made.

Although we agree that similar mechanisms can underlie implicit and explicit memory expressions in some circumstances, we adhere to the key position we took in our article—the *assumption* that familiarity experiences mediate the relationship between fluency and recognition decisions in any given situation must not be accepted without sufficient evidence. For example, the Jacoby and Whitehouse (1989) findings using masked priming of recognition test cues are frequently invoked as evidence for fluency attribution accounts, particularly when taken together with subsequent findings that masked priming affects "Know" but not "Remember" responses. However, the option to "guess" or to rate decision confidence is seldom offered. As described in our target article, "Know" decisions under such circumstances may function as a catch-all category that includes not only responses associated with familiarity, but also guess responses that stem from implicit memory processing. Interestingly, one study that did include an option to guess (Tunney & Fernie, 2007) showed that masked priming increased the percentage of old responses that were guesses, and not those associated with familiarity or recollection. Without the "guess" response option, the influence of implicit memory likely would have been erroneously attributed to familiarity. In a similar vein, Hayes and Verfaellie pointed out interesting ways in which the influence of fluency on "guess" responses is reminiscent of effects of fluency on recognition performance in amnesic patients. For example, Verfaellie, Giovanello, and Keane (2001) found that encouraging a liberal response criterion improved memory discrimination in amnesic patients. Whereas these and similar findings are often interpreted as influences on familiarity, it is plausible that implicit recognition is at work instead. Indeed, we have found that liberal encouragement increases implicit recognition indicated with the "guess" option but has no influence on familiarity experiences separate from guessing (Voss & Paller, 2010).

It is important to emphasize that showing that a manipulation selectively affects "Know" or some general measure of non-recollective "old" responses is not the same as showing that its effect is selective to familiarity. The research we described in our target article illustrated that other mechanisms can produce such effects without involving experiences of familiarity. Of course, these findings are in no way at odds with the notion that fluency can contribute to familiarity experiences under certain circumstances, and we agree with Hayes and Verfaellie that identifying the factors that modulate whether fluency leads to implicit recognition versus familiarity is an exciting topic for future research.

We suggest that our ability to answer these and other questions about relationships between implicit and explicit memory hinges on our ability to separate their respective neural signals. In our target article, we describe dissociations indicating that neural signals of familiarity can be reliably separated from those related to perceptual and conceptual fluency. The commentary by Wilding critiqued some of the specific data points we used to support the distinction between familiarity and conceptual fluency. In several experiments, we linked FN400 ERPs with conceptual fluency, contradicting a widespread (and, we argue, incorrect) notion that FN400 potentials index a generic familiarity signal. Specifically, we reviewed evidence that: (1) Associations between FN400 potentials and familiarity during recognition were limited to situations in which concurrent conceptual fluency effects were likely, and (2) FN400 potentials correlated with behavioral measures of conceptual fluency on priming tests, whereas other ERPs (the late-positive complex) correlated with behavioral measures of familiarity. Thus, our position is that FN400 potentials reflect conceptual fluency and do not directly or universally reflect familiarity.

Wilding expressed two concerns about this conclusion. The first was whether our studies were successful in matching familiarity between situations that did and did not permit conceptual fluency. Second, Wilding cited findings that seem to contradict our interpretations (Stenberg, Hellman, Johansson, & Rosén, 2009). Because behavioral measures of familiarity are imperfect, there cannot be complete certainty that our neural contrasts of conditions in which familiarity occurred with versus without conceptual fluency were 100% matched. Nevertheless, much of the evidence we described contradicts the interpretation that our reported dissociations between conceptual fluency and familiarity were due to subtle differences in familiarity. Some stimuli fail to evoke meaningful associations but can still be recognized. We found that such meaningless stimuli unquestionably supported familiarity-based recognition, yet did not produce FN400 ERPs. For stimuli that were not conceptually meaningful in the study by Voss, Lucas, and Paller (2010), for example, high-confidence "Know" hits outnumbered false alarms by a factor of nine, and yet no FN400 effects were present when these trials were compared with correct rejections (CRs). Thus, FN400 potentials cannot provide a reasonable index of familiarity for these words. In contrast, familiarity-based recognition for conceptually meaningful items in our study occurred with indistinguishably different accuracy, yet *was* associated with robust FN400 effects. Our target article also describes converging evidence from other labs and paradigms that stimuli that are devoid of conceptual fluency yet recognized with familiarity do not produced FN400 effects. For these reasons, we do not share the concern expressed by Wilding about our findings, though we agree that there is value in continuing to find new ways to dissociate familiarity from conceptual fluency.

Regarding Wilding's second concern, we appreciate that Stenberg and colleagues (2009) attempted to dissociate ERP correlates of familiarity and conceptual fluency, but we remain skeptical of their interpretations due to methodological shortcomings (Lucas, Voss, & Paller, 2010). Their conclusions rest on the problematic assumption that conceptual fluency was not facilitated by repetition of non-famous names. If this assumption were correct, then a dissociation between FN400 and conceptual fluency would have been achieved through the finding that FN400 differences between hits and CRs for non-famous names did not differ significantly from the corresponding contrast for famous names. On the contrary, participants taking memory tests frequently manufacture meaning for initially unfamiliar stimuli as an intuitive mnemonic strategy, such that unfamiliar stimuli perceived as meaningful can reliably and robustly support conceptual priming (e.g., Voss & Paller, 2007; Voss et al, 2010; Voss, Schendan, & Paller, 2010) as well as neural repetition effects in brain regions that closely match effects of conceptual priming for real objects and words (Voss, Federmeier, & Paller, in press). Moreover, it is precisely those stimuli for which meaning is successfully invoked that are likely to be remembered later. Thus, the use of Hit/CR contrasts to examine familiarity in non-famous names surely led to the selective inclusion of trials corresponding to the names that held the most meaning for each participant—in other words, the names with the capacity to support conceptual fluency and cue successful recognition.

Although Stenberg and colleagues did attempt to verify their claim that conceptual fluency was enhanced only for repeated famous names using priming tests of speeded fame and frequency, only one of these tests—speeded fame judgments—evinced priming for either category of names. Whereas this priming was indeed selective to famous names, it is logical to question the utility of this measure for indexing analogous priming for both types of stimuli given that famous and non-famous names require opposite responses in order to be correct on a fame judgment task. Should fluency with non-famous names be expected to facilitate their identification as non-famous? In fact, fluency in this context might lead to at least some degree of a false sense of fame for non-famous names, thus impairing performance. Furthermore, a second pillar of the arguments of Stenberg and colleagues—the finding that FN400 potentials, but not priming effects, were greater for low-frequency relative to high-frequency names—should be regarded with caution given the known effects of frequency on conceptual priming for words. Repetition of low-frequency words produces greater facilitation on priming tests when compared to repetition of high-frequency words (e.g., Duchek & Neely, 1989; Forster & Davis, 1984; Scarborough, Cortese, & Scarborough, 1977) and there is little reason to suspect that this would not also be the case for names. Accordingly, we remain unconvinced by Stenberg and colleagues' findings, but sympathize with Wilding's call for further investigation of this issue.

In summary, these discussions illustrate that there is merit in putting further effort toward dissociating explicit recognition memory from fluency in order to study these phenomena in isolation (see also the comment by Stark for a reminder of the ways that such dissociations have contributed to our understanding of memory disorders). These efforts will remain relevant even as we follow the advice put forth by Eichenbaum, Stark, and other commentators to begin to "fill in the gaps" left by dissociations by focusing on interactions among memory systems.

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