Published in final edited form as:

Cogn Neurosci. 2012 ; 3(0): 193–207. doi:10.1080/17588928.2012.674935.

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

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Abstract

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

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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 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 odors (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 odors 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 below¹). 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

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¹Note 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.

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 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

²There 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.

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 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.

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 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 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

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³Note 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.

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 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.

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TRENDS in Cognitive Sciences

Figure 1.

Repetition influences many types of neurocognitive processing. Viewing a simple stimulus engages a multitude of neuro-cognitive 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.

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.

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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.

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