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Many roads lead to recognition: Electrophysiological correlates of familiarity derived from short-term masked repetition priming

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ABSTRACT

The neural mechanisms that underlie familiarity memory have been extensively investigated, but a consensus understanding remains elusive. Behavioral evidence suggests that familiarity sometimes shares sources with instances of implicit memory known as priming, in that the same increases in processing fluency that give rise to priming can engender familiarity. One underappreciated implication of this account is that patterns of neural activity that appear to index familiarity in a generic sense may instead reflect fluency-related precursors of recognition. In a novel illustration of this principle, we examined brain potentials during recognition tests for visual words. In two experiments, fluency was selectively enhanced for half of the test cues via masked repetition priming. Replicating previous findings, the proportion of words endorsed as “old” was greater for words immediately preceded by a matching masked word versus an unrelated one. In addition, N400 potentials were more positive for test cues preceded by matching versus unrelated masked words. Similar N400 differences were observed when false alarms were compared to correct rejections for the subset of unstudied words that were preceded by matching masked words. These N400 effects were topographically dissociable from other potentials that correlated with familiarity for studied words. We conclude that experiences of familiarity can have different neural correlates that signal the operation of distinct neurocognitive precursors of recognition judgments. Conceptualizations of the neural basis of recognition memory must account for a plurality of mechanisms that produce familiarity memory.

1. Introduction

Dual-process theories of recognition memory posit that recognition decisions can be supported by either familiarity or recollection (Aggleton & Brown, 2006; Eichenbaum, Yonelinas, & Ranganath, 2007; Mandler, 1980; Yonelinas, 2002). *Familiarity* refers to the impression that a stimulus has been previously encountered that is unsubstantiated by the retrieval of any relevant contextual details. For example, familiarity would support a conviction that a woman's face had been encountered previously, even without any further recall. By contrast, *recollection* implies that contextual or other details regarding the prior event are also recalled, such as the woman's name or the location of a prior encounter.

Extensive research efforts have recently been focused on understanding the neural processes that support recollection and familiarity. However, fundamental questions germane to this topic remain open. Whereas recollection is often believed to operate via a categorical or threshold process (e.g., Yonelinas, 1994; Yonelinas & Parks, 2007), most characterizations of familiarity posit a signal-detection process by which a global match is computed between a test cue and stored memory traces (Hintzman, 1988; Norman, 2010; Shiffrin & Steyvers, 1997). As such, patterns of neural activity that vary continuously with the strength of subjective familiarity experiences are often presumed to index this summation. However, it has been argued that recollection can also be graded or continuous, such that familiarity and weak recollection are difficult to dissociate (Slotnick, 2010; Wixted, 2007; Wixted, Mickes, & Squire, 2010). In addition, certain forms of implicit memory exhibit properties that are very similar to those of familiarity (for reviews, see Paller, Voss, & Boehm, 2007; Yonelinas, 2002). As a result, questions have been raised about the extent to which patterns of neural activity that have previously been attributed to familiarity in neuroimaging studies may instead reflect forms of implicit memory, such as enhanced fluency at conceptual or perceptual levels of processing (Voss & Paller, 2007; Voss, Hauner, & Paller, 2009; Voss, Lucas, & Paller, 2010a; Wang, Lazzara, Ranganath, Knight, & Yonelinas, 2010).

The last of these concerns relates to broader questions about the relationship between familiarity and *priming*, an expression of implicit or nonconscious memory observed in various types of

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specialized tests. Substantial evidence suggests that the same fluency signals that give rise to priming can sometimes guide conscious recognition memory (Cleary, 2004; Jacoby & Whitehouse, 1989; Parkin et al. 2001; Westerman, Lloyd, & Miller, 2002; Westerman, Miller, & Lloyd, 2003). For example, in a pioneering study, Jacoby and Whitehouse (1989) gave participants recognition memory tests for words. Unbeknownst to the participants, each test word was preceded by a 50-ms, masked presentation of a prime word that was either the same as the upcoming test word (here termed *masked-prime same* or *MP-same* trials), or a different word (here termed *masked-prime different* or *MP-different* trials). Although participants were unable to identify the prime words, the probability of a subsequent "old" decision was higher on MP-same relative to MP-different trials[1]. Moreover, findings from subsequent research suggest that this and similar fluency manipulations disproportionately influence familiarity as opposed to recollection (Miller, Lloyd, & Westerman, 2008; Rajaram & Geraci, 2000; Woollams, Taylor, Karayanidis, & Henson, 2008; but see Brown & Bodner, 2011; Kurilla & Westerman, 2008; Taylor & Henson, this issue). These and related findings support a fluency-attribution account of familiarity, according to which feelings of familiarity can reflect an unconscious inference about the source of fluent processing rather than a direct product of an underlying memory trace (Jacoby & Dallas, 1981).

One important but underappreciated implication of this theoretical account is that the neural correlates of familiarity are likely to differ according to the extent and types of fluency from which each instance of familiarity is derived. Indeed, priming is known to have multiple subtypes driven by dissociable forms of fluency, the most well-studied of which are conceptual and perceptual fluency (Henson, 2003; Schacter, Wig, & Stevens, 2007). In a recent review, Alter and Oppenheimer (2009) catalogued at least four additional subtypes of fluency for linguistic stimuli alone, including phonologic, lexical, syntactic, and orthographic fluency, and argued that manipulating fluency along any of these dimensions can produce essentially the same behavioral outcome within a given domain of judgment, including judgments of familiarity. It is thus perhaps surprising that familiarity tends to be discussed and operationalized as an amodal or unitary neural construct. Indeed, neuroimaging methods have typically been employed in search of generic familiarity markers, most often with the goal of establishing double dissociations between familiarity and recollection in order to provide evidence in favor of dual-process models of recognition. As such, steps are rarely taken to determine whether patterns of neural activity that covary with familiarity are more closely tied to one or more potential precursors of recognition.

Importantly, dual-process models may not be adequately captured by neural double-dissociations if familiarity has a variable relationship to multiple underlying memory signals. This notion may help to reconcile current controversies concerning putative neural correlates of familiarity. For instance, a popular but controversial position within the literature on event-related potentials (ERPs) has been that familiarity and recollection can be doubly dissociated through specific brain potentials known as FN400 and LPC, respectively. However, FN400 potentials are found in conjunction with familiarity for meaningful or verbalizable stimuli—such as words or nameable pictures—but generally not for nonverbal stimuli such as abstract patterns or nonsense words, even when these items evoke strong familiarity (Danker et al., 2008; Voss & Paller, 2007; Voss et al., 2010a). Several explanations have been proposed as to why the association between FN400 and familiarity breaks down in situations that are not amenable to conceptual stimulus processing. For example, some have suggested that conceptual processing simply engenders larger amounts of familiarity or increases reliance on familiarity relative to nonconceptual processing (e.g., Danker et al., 2008; Meyer, Mecklinger, & Friederici, 2007). Others have proposed that FN400 potentials reflect conceptual fluency that occurs incidentally during recognition tests, and that LPC potentials reflect both recollection and familiarity per se (e.g., Voss & Paller, 2007; Voss et al., 2010a). Interestingly, fluency-attribution accounts of familiarity suggest a different hypothesis that has received little attention, which is that FN400 reflects a conceptual fluency-related *precursor* to familiarity. In other words, FN400 effects may often—but not always—correlate with familiarity because familiarity is often—but not always—derived from conceptual fluency. In addition to reconciling the aforementioned familiarity literature, this account can accommodate findings that FN400 potentials correlate with conceptual priming (Voss & Paller, 2006; Voss, Schendan, & Paller, 2010b).

It is difficult to probe neural correlates of conceptual fluency in isolation from familiarity because the conditions most suitable for producing conceptual fluency—such as repetition following deep or meaning-based encoding—often also produce familiarity. Thus, findings that similar ERPs are elicited during tests of conceptual priming and tests of familiarity could indicate a shared fluency source, but could also reflect contamination by one form of memory during tests intended to capture the other. Fluency-attribution accounts predict that whenever any fluency—including perceptual or lexical fluency—is attributed to prior exposure, its neural measures will be coupled with the resulting feeling of familiarity. As previously mentioned, these forms of fluency can be reliably achieved using masked priming manipulations, which can also provide behavioral evidence of the influence of this fluency on recognition decisions. The present research thus seeks further evidence to adjudicate on these issues by examining electrophysiological correlates of familiarity in situations wherein its source can be convincingly tied to fluency induced by masked-priming methods.

Our research strategy extends that used by Woollams et al. (2008), in which masked repetition priming of recognition test words was combined with EEG recordings. By analyzing ERPs, Woollams and colleagues were able to compare neural correlates of masked priming with those of familiarity for previously studied words. As predicted, masked priming was associated with increased familiarity (as assessed in a Remember/Know paradigm, a method for measuring recollection and familiarity via metacognitive judgments, Rajaram, 1993). Also, a comparison of familiar hits with misses, collapsed across MP-same and MP-different trials, revealed the expected FN400 effect. Although masked priming served to increase familiarity, it did not influence FN400 potentials, as would be expected if FN400 were a generic or universal index of familiarity. Rather, MP-same trials were associated with central ERPs from 150–250 ms as well as with posterior N400 potentials.

These findings support the idea that familiarity can be multiply determined, in that multiple neural signals were associated with familiarity. However, there were limitations of the extent to which ERPs associated with masked priming could be linked to the influence of masked priming on recognition. Indeed, these ERPs did not interact with behavioral indices of recognition memory, but rather were similar across recollection hits, familiarity hits, and correct rejections. These ERPs may thus have

[1] Although this procedure has typically been employed with the intention to enhance perceptual fluency (e.g., Huber, Clark, Curran, & Winkielman, 2008; Kurilla & Westerman, 2008; Westerman, 2008; Westerman et al. 2002, 2003; Willems, Germain, Salmon, & Van der Linden, 2009), the extent to which conceptual fluency is enhanced by the matching masked prime words is unclear. With paradigms used to assess performance on lexical decision and other priming tasks following masked priming, effects tended to be more robust and reliable on lexical and pre-lexical levels than on semantic levels (Holcomb, Reder, Misra, & Grainger, 2005; Schnyer, Allen, & Forster, 1997). A likely generalization, then, is that effects of masked repetition priming on recognition memory in large part reflect fluency at pre-conceptual levels.