Manipulating letter fluency for words alters electrophysiological correlates of recognition memory

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ABSTRACT

The mechanisms that give rise to familiarity memory have received intense research interest. One current topic of debate concerns the extent to which familiarity is driven by the same fluency sources that give rise to certain implicit memory phenomena. Familiarity may be tied to conceptual fluency, given that familiarity and conceptual implicit memory can exhibit similar neurocognitive properties. However, familiarity can also be driven by perceptual factors, and its neural basis under these circumstances has received less attention. Here we recorded brain potentials during recognition testing using a procedure that has previously been shown to encourage a reliance on letter information when assessing familiarity for words. Studied and unstudied words were derived either from two separate letter pools or a single letter pool ("letter-segregated" and "normal" conditions, respectively) in a within-subjects contrast. As predicted, recognition accuracy was higher in the letter-segregated relative to the normal condition. Electrophysiological analyses revealed parietal old–new effects from 500–700 ms in both conditions. In addition, a topographically dissociable occipital old–new effect from 300–700 ms was present in the letter-segregated condition only. In a second experiment, we found that similar occipital brain potentials were associated with confident false recognition of words that shared letters with studied words but were not themselves studied. These findings indicate that familiarity is a multiply determined phenomenon, and that the stimulus dimensions on which familiarity is based can moderate its neural correlates. Conceptual and perceptual contributions to familiarity vary across testing circumstances, and both must be accounted for in theories of recognition memory and its neural basis.

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Introduction

The simplest expression of memory for a prior episode is the experience of recognizing something as familiar. Contemporary theories of recognition memory emphasize the distinction between familiarity and another mnemonic expression termed recollection (Aggleton and Brown, 2006; Eichenbaum et al., 2007; Mandler, 1980; Yonelinas, 2002). Recollection refers to a recognition experience accompanied by the ability to recall the spatiotemporal context or other specific features of a previous encounter—for example, when recognizing an acquaintance and recalling her name, or seeing a photograph and identifying the circumstances under which it was taken. By contrast, familiarity refers to the impression that a particular stimulus has been encountered previously without substantiation by the recall of relevant details.

The notion that distinct neurocognitive processes subserve recognition with and without recollection has been extremely influential in recent years. This distinction has been particularly useful in identifying properties that disproportionately characterize recollection. For example,

there is now substantial evidence that recollection depends on hippocampal processing (Aggleton and Brown, 1999; Eichenbaum et al., 2007), that it is diminished when attentional resources are challenged (Troyer et al., 1999; Yonelinas, 2001), and that it is susceptible to impairment in a variety of neurological and psychiatric disorders such as Alzheimer's Disease, mild cognitive impairment (MCI; Anderson et al., 2008; Westerberg et al., 2006), and schizophrenia (Danion et al., 2007; Huron et al., 1995). By contrast, there is far less consensus on many of these issues with regard to familiarity (Algarabel et al., 2009a; Cipolotti et al., 2006; Jacoby and Kelley, 1992; Libby et al., 2013; Weiss et al., 2008; Wixted and Squire, 2004; Wolk et al., 2005). Moreover, disagreements abound regarding the neural correlates of familiarity in healthy individuals when measured with event-related potentials (ERPs: e.g., Paller et al., 2007; Rugg and Curran, 2007; Voss and Federmeier, 2011) and functional neuroimaging (fMRI: e.g., Cowell et al., 2010; Ranganath et al., 2004; Wais et al., 2006).

Given that familiarity is notoriously difficult to measure and to separate from recollection, oftentimes discrepant findings in the literature may be attributable to differences in measurement techniques (Libby et al., 2013; Paller et al., 2007; Wixted et al., 2010; Yonelinas, 2002) or, when applicable, in patient type or severity (Algarabel et al., 2009a; Bastin et al., 2013; Yonelinas et al., 2010). However, there is

also evidence that familiarity performance—even when measured in the same individuals in the same manner—can vary according to the stimulus dimensions that are most relevant and/or salient during a particular task. For example, Embree, Budson, and Ally (2012) found that familiarity in a group of patients with MCI was intact for pictures, but impaired for words, a finding that roughly mirrors the general pattern in the literature (for review, see Ally, 2012). In addition, a patient with a left perirhinal cortex lesion who was initially characterized as having a general familiarity deficit (Bowles et al., 2007) was recently found to have intact familiarity for nonverbal stimuli, such as faces and abstract line drawings (Martin et al., 2011). Electrophysiological correlates of familiarity can also differ depending on the stimuli for which familiarity is measured. It has been widely assumed that familiarity can be generically indexed by a particular brain potential termed FN400 (e.g., Rugg and Curran, 2007). However, FN400 potentials usually correlate with familiarity when it occurs for words or nameable pictures but not when it occurs for nonverbalizable stimuli such as complex geometric patterns or faces (Danker et al., 2008; Voss et al., 2010a; Voss and Paller, 2007, 2009b; Yovel and Paller, 2004).

Why might familiarity—which can be strikingly amodal from a phenomenological standpoint—appear to be heterogeneous on a neural level? Findings from our laboratory and others suggest that one key to deconstructing familiarity lies in a closer examination of its relationship to the implicit memory phenomena of priming (Dew and Cabeza, 2011; Leynes and Zish, 2012; Lucas et al., 2012; Wang et al., 2010; Wang and Yonelinas, 2012; Woollams et al., 2008). Priming occurs when prior experience results in an increase in the fluency with which specific stimuli are processed and thereby facilitates certain responses or decisions about these stimuli. It has long been suggested that the same fluency signals thought to give rise to priming can also contribute to familiarity experiences (Jacoby and Dallas, 1981), though the extent and nature of these contributions remain an open topic of study.

Importantly, it is generally well-appreciated that priming is multifaceted in its neural underpinnings. The spatial and temporal loci of the repetition-related boosts in fluency that lead to priming are known to depend on the nature of the relevant stimulus representations. Repetition priming for visual stimuli, for example, can be registered at various points along a posterior-to-anterior gradient within the ventral visual processing stream, with posterior regions computing information about lower-level sensory information and anterior regions computing information about global form, structure, and meaning (e.g., Henson, 2003; Schacter et al., 2007). These regions also tend to be unevenly susceptible to the neuropathology of Alzheimer's Disease and MCI, such that conceptual priming impairments are evident earlier and to a greater degree than perceptual priming impairments (Fleischman et al., 2005). Thus, insofar as familiarity can sometimes be an outcome of fluency, one would expect its neurocognitive basis to also show an amount of representational specificity. In particular, the research presented here examines the possibility that differential contributions of certain types of fluency to familiarity across experimental situations can account for discrepant findings in prior investigations.

We have previously argued (Lucas et al., 2012; Paller et al., 2007; Voss et al., 2012) that our understanding of familiarity and its neural basis is limited by the fact that most studies of familiarity have used stimuli that are replete with meaning, such as words and nameable pictures. As a result, neural measures such as FN400 potentials that appear to track stimulus familiarity per se may instead reflect increases in conceptual fluency that occur upon stimulus repetition. Indeed, conceptual fluency and familiarity may often be tightly correlated across trials—and their neural correlates thus highly confusable—because trial-to-trial fluctuations in factors such as attention and depth-of-encoding can exert parallel influences on both outcomes (Paller et al., 2007; Yonelinas, 2002). Moreover, evidence from our laboratory suggests that FN400 potentials covary more closely and reliably with conceptual priming than they do with familiarity (Voss et al., 2010a, 2010b; Voss and Paller, 2007; Voss et al., 2010b). Whereas this research has

generally been silent about whether conceptual fluency contributes to familiarity, findings using individual-difference and lesion-mapping approaches to compare the two phenomena (Wang et al., 2010; Wang and Yonelinas, 2012) are suggestive of a shared underlying mechanism when familiarity is based on conceptual stimulus dimensions. By comparison, the neural mechanisms of familiarity based on perceptual stimulus dimensions remain relatively unexplored. Given that many neurocognitive attributes of conceptual fluency do not apply to perceptual fluency, one might not expect findings about conceptually-driven familiarity to generalize to other situations. Investigations of familiarity in a more diverse set of circumstances—particularly circumstances in which familiarity is supported by relatively low-level stimulus features—will be necessary to gain a more precise and comprehensive view of familiarity memory and its neurocognitive properties.

A paradigm introduced by Parkin et al. (2001) seems promising in this regard. This paradigm capitalizes on the fact that processing fluency for words can be enhanced through exposure to their component lower-level elements, such as individual letters or letter clusters (Dehaene et al., 2004). Due to the limited number of letters and common letter combinations in most languages, fluency with letter information is inadequate for differentiating between studied and unstudied words in typical recognition tests. To investigate whether familiarity could be driven by these perceptual characteristics under certain circumstances, Parkin and colleagues investigated recognition for target and lure stimuli constructed from entirely separate pools of letters. In the key condition of this study—here termed the Letter-Segregated (LS) condition—target words were derived from a restricted set of letters and lures were derived from a different, non-overlapping letter set. In a second condition—here termed the Normal (N) condition—targets and lures were derived from the entire alphabet, as is normally the case in recognition memory experiments. The logic of this design was that information concerning low-level stimulus dimensions that correspond to letters would be available as a cue to recognition only in the LS condition. As predicted, Parkin and colleagues found that recognition memory was enhanced in the LS relative to the N condition. Moreover, this finding obtained even though subjects reported being unaware of the experimental manipulation, suggesting that they did not use a recollective strategy to discriminate the different letters that comprised targets and lures in the LS condition. Presumably, the memory improvement in the LS condition was due to familiarity derived from letter fluency (see also Algarabel et al., 2009b; Algarabel and Pitarque, 2010; Bastin et al., 2013; Keane et al., 2006, for similar arguents).

In the present research, we combined the letter-segregation paradigm with recordings of ERPs in order to investigate the neural basis of familiarity driven by letter information. In Experiment 1, we neurally isolated contributions of letter fluency to recognition by analyzing ERPs for correctly recognized studied words (hits) and correctly rejected unstudied words (CRs) in the LS and N conditions. The logic of the analysis strategy was that fluency with conceptual information should differ to roughly the same extent between targets and lures in both conditions, whereas fluency with sublexical information—and its associated neural correlates—will correspond to prior exposure only in the LS condition. Because FN400 effects are generally observed only when familiarity co-occurs with conceptual fluency, we did not expect FN400 potentials to differ between the LS and N conditions. Rather, other ERPs should be associated with enhanced recognition due to letter fluency, perhaps including posterior ERPs associated with implicit memory for words or word components (Grainger and Holcomb, 2009; Paller and Gross, 1998; Rugg et al., 1998). In Experiment 2, we attempted to replicate and extend the findings obtained in Experiment 1 by altering the paradigm to examine ERPs to false alarms for words that were not presented in the study phase, but that shared letters with words that were presented in the study phase.

As in prior studies that have used this letter-segregation paradigm, data from participants who evinced any knowledge of the letter