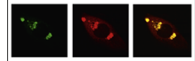


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Research Report

Familiarity and priming are mediated by overlapping neural substrates



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ABSTRACT

Explicit memory is widely assumed to reflect the conscious processes of recollection and familiarity. However, familiarity has been hypothesized to be supported by nonconscious processing. In the present functional magnetic resonance imaging (fMRI) experiment, we assessed whether familiarity is mediated by some of the same regions that mediate repetition priming, a form of nonconscious memory. Participants completed an implicit (indirect) memory task and an explicit (direct) memory task during fMRI. During phase I of each task, participants viewed novel abstract shapes with internal colored oriented lines and judged whether each shape was relatively “pleasant” or “unpleasant”. During phase II of the indirect memory task, repeated (old) and new shapes were presented and participants made the same judgments. During phase II of the direct memory task, a surprise recognition test was given in which old and new shapes were presented and participants made “remember”, “know”, or “new” responses. Activity associated with priming was isolated by comparing novel versus repeated shapes during phase II of the indirect memory task. Activity associated with familiarity was isolated by comparing accurate “know” responses versus misses during phase II of the direct memory task. Priming and familiarity were associated with common activity within the superior parietal lobule and motor cortex, which we attribute to shared attentional and motor processing, respectively. The present fMRI results support the hypothesis that familiarity is supported by some of the same processes that support implicit memory.

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Introduction

Explicit memory is widely assumed to reflect the conscious processes of recollection and familiarity (for reviews, see Rugg, 1995; Yonelinas, 2002; Paller et al., 2009; Dew and Cabeza, 2011). Recollection reflects consciously accessible

information about both the prior occurrence of an item and its associated context and familiarity reflects confidence of the prior occurrence of an item in the absence of qualitative information about the prior occurrence (Mandler, 1980; Yonelinas, 2002). The processes of recollection and familiarity are commonly operationalized in the laboratory using the

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remember/know task. In this task, a “remember” response signifies conscious retrieval of specific details of the prior episode and a “know” response signifies confidence in the recognition of an item without the retrieval of specific details (Tulving, 1985).

Although familiarity-based recognition is often used as an index of conscious memory, there is a longstanding hypothesis that familiarity is supported by some of the same processes that subserve implicit (nonconscious) memory (e.g., Mandler, 1980; Jacoby and Dallas, 1981; Jacoby, 1991; Yonelinas, 2002; but see, Voss et al., 2012; for a review, see Dew and Cabeza, 2011). One such process is repetition priming. Priming is a form of memory that reflects increases in behavioral performance (e.g., speeded reaction times) due to the repeated presentation of an item, and such behavioral changes do not depend on awareness of the prior occurrence (Schacter and Buckner, 1998; Henson, 2003; Schacter et al., 2004, 2007). These facilitations in behavioral performance have been attributed to three processes: perceptual, conceptual, or response-related priming (for a review, see Henson et al., 2014). Perceptual priming refers to facilitations in processing the physical attributes of a repeated stimulus. Conceptual priming refers to facilitations in processing the semantic attributes of a repeated stimulus (e.g., stimulus meaning). Response priming refers to the facilitation in processing related to making the same motor response/decision to a repeated stimulus. Although the precise neural mechanisms supporting these various behavioral facilitations are under active investigation (see, Gotts et al., 2012; Henson, et al., 2014), one common observation is that the behavioral priming effects are associated with decreased neural activity for repeated relative to novel stimuli. These neural priming effects are typically observed in regions associated with processing the stimulus information that is repeated (e.g., priming for visual information is largely observed in visual sensory cortex; for reviews, see Schacter and Buckner, 1998; Henson, 2003; Schacter et al., 2004, 2007).

Several studies have provided behavioral evidence that both familiarity and priming may be supported by some of the same underlying mental processes (for reviews, see Wagner and Gabrieli, 1998; Kelley and Rhodes, 2002; Yonelinas, 2002; Dew and Cabeza, 2011). For example, in the masked perceptual priming paradigm, recognition test items are preceded by masked presentations of the same test item or a different item. Rates of familiarity (“know” responses) increase when test items are masked versus unmasked (e.g., Rajaram, 1993; Woollams et al., 2008; Taylor and Henson, 2012; Taylor et al., 2013). Performance on conceptual priming tasks (e.g., a free association task) has also been shown to be correlated with familiarity-based recognition (Wang and Yonelinas, 2012; but see, Taylor and Henson, 2012; Taylor et al., 2013). These findings suggest that the same processes that lead an item to be more fluently processed on a priming task may also lead an item to be judged as familiar on a recognition memory test.

A number of event-related potential (ERP) studies have examined whether familiarity and priming are mediated by similar neural processes (e.g., Woollams et al., 2008; Lucas et al., 2012; for a review see, Voss et al., 2012). In one study that employed a masked perceptual priming paradigm (Lucas et al., 2012), ERP correlates associated with familiarity were

qualitatively distinct from those associated with masked priming. However, the ERP correlates associated with masked priming were also correlated with behavioral measures of familiarity (i.e., “know” responses). For example, the ERP effect that discriminated masked and unmasked trials also discriminated trials where participants made “know” responses relative to “new” responses. These findings suggest there are common neural processes associated with priming and familiarity.

As ERPs have limited spatial resolution, different neural regions may be contributing to the apparent ‘common’ ERP effect. Of relevance to this point, to our knowledge, there have been only three functional magnetic resonance imaging (fMRI) studies that have examined the extent to which the neural correlates of priming and familiarity overlap. During a conceptual priming task (Voss et al., 2008), participants discriminated famous and non-famous faces. During the explicit memory task, participants discriminated old and new faces using “remember”, “know”, or “new” responses. Conceptual priming, identified with the contrast of primed versus unprimed faces, was associated with decreases in activity within the prefrontal cortex, while familiarity, identified with the contrast of “know” responses to old faces versus new faces, was associated with increases in activity within the parietal cortex. Note that the contrast used to isolate familiarity was confounded by study status (i.e., old versus new faces) and thus the putative familiarity-related activity could have reflected priming related processes (cf., Slotnick and Schacter, 2007). In a more recent fMRI study (Wang et al., 2014), participants completed a free-association conceptual priming task with words as stimuli. In a separate explicit memory task, participants judged the study status of old and new words using a 6-point confidence scale. In contrast to the dissociation reported by Voss et al. (2008), Wang et al. (2014) reported overlapping neural activity associated with conceptual priming and familiarity in the perirhinal cortex. In this study, however, familiarity and recollection were assumed to simply differ in their confidence (i.e., low versus high confidence responses, respectively). Thus, as there was no response category to appropriately segregate recollection-based recognition, recollection may have occurred at the confidence responses assumed to reflect familiarity (i.e., low confidence responses). Lastly, in Taylor et al. (2013) a masked priming paradigm was employed (see above). Across the neural regions identified to be familiarity-related (isolated with the contrast of “know” responses to old items relative to new items), no effects of priming were observed.

Although there has been ERP evidence supporting the hypothesis that there are shared neural processes associated with familiarity and priming (e.g., Lucas et al., 2012), the extant fMRI evidence has been inconclusive. The aim of the present fMRI study was to test the hypothesis that familiarity is supported by some of the same processes that support priming. Specifically, we sought to determine whether the neural correlates of familiarity and priming would overlap. Evidence of overlapping neural correlates would provide evidence that familiarity and priming are mediated by shared mechanisms. However, if priming and familiarity were mediated by non-overlapping neural substrates, this would indicate that these

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