Brain and Cognition 91 (2014) 11–20

Contents lists available at ScienceDirect

Brain and Cognition

journal homepage: www.elsevier.com/locate/b&c

The temporal dynamics of visual object priming

Philip C. Ko [a,*], Bryant Duda [a], Erin P. Hussey [a], Emily J. Mason [a], Brandon A. Ally [a,b,c]

[a] Department of Neurology, Vanderbilt University, Nashville, TN 37232, United States
[b] Department of Psychiatry, Vanderbilt University, Nashville, TN 37232, United States
[c] Department of Psychology, Vanderbilt University, Nashville, TN 37232, United States

ARTICLE INFO

Article history:
Accepted 30 July 2014

Keywords:
Priming
Neural suppression
Event-related potentials
Implicit memory

ABSTRACT

Priming reflects an important means of learning that is mediated by implicit memory. Importantly, priming occurs for previously viewed objects (item-specific priming) and their category relatives (category-wide priming). Two distinct neural mechanisms are known to mediate priming, including the sharpening of a neural object representation and the retrieval of stimulus–response mappings. Here, we investigated whether the relationship between these neural mechanisms could help explain why item-specific priming generates faster responses than category-wide priming. Participants studied pictures of everyday objects, and then performed a difficult picture identification task while we recorded event-related potentials (ERP). The identification task gradually revealed random line segments of previously viewed items (Studied), category exemplars of previously viewed items (Exemplar), and items that were not previously viewed (Unstudied). Studied items were identified sooner than Unstudied items, showing evidence of item-specific priming, and importantly Exemplar items were also identified sooner than Unstudied items, showing evidence of category-wide priming. Early activity showed sustained neural suppression of parietal activity for both types of priming. However, these neural suppression effects may have stemmed from distinct processes because while category-wide neural suppression was correlated with priming behavior, item-specific neural suppression was not. Late activity, examined with response-locked ERPs, showed additional processes related to item-specific priming including neural suppression in occipital areas and parietal activity that was correlated with behavior. Together, we conclude that item-specific and category-wide priming are mediated by separate, parallel neural mechanisms in the context of the current paradigm. Temporal differences in behavior are determined by the timecourses of these distinct processes.

1. Introduction

Substantial evidence of learning can be observed after a single encounter with a visual object. Repeated encounters result in facilitated behavior, or *priming*, like faster naming or categorization of the object. Priming occurs without the subjective re-experiencing of the initial encounter, indicating that it is mediated by *implicit memory* rather than explicit memory (Voss & Paller, 2008). Any form of learning must discriminate repeated encounters with objects as "different" or the "same", but the shared perceptual and conceptual features of objects from the same category, like "dogs", pose a challenge to this cognitive ability. For example, a retriever and Pomeranian are very "different" in size and appearance, but they are also the "same" since they are both furry and have four legs. Implicit memory is sensitive to the shared perceptual and conceptual features of category members, as demonstrated by results showing priming for the repetition of a previously viewed object as well as a category relative, or *exemplar*, of a previously viewed object (Marsolek, 1999; Marsolek & Burgund, 2008). In other words, implicit memory represents objects on *item-specific* and *category-wide* levels.

Do common or distinct neural processes mediate item-specific and category-wide priming? Research has made headway in addressing this problem, but has not related neural findings to a consistent behavioral result: while both repetitions and exemplars elicit faster responses than novel items, repetitions elicit faster responses than exemplars (Cave, Bost, & Cobb, 1996; Chouinard, Morrissey, Köhler, & Goodale, 2008; Francis, Corral, Jones, & Sáenz, 2008; Stevens, Kahn, Wig, & Schacter, 2012). In other words, item-specific priming is generally faster than category-wide priming. How can this pattern of behavioral priming be explained?

The relationship between item-specific and category-wide priming may be understood by considering the involvement of

* Corresponding author. Address: Department of Neurology, A-0118 Medical Center North, 1161 21st Avenue South, Nashville, TN 37232, United States. Fax: +1 (615) 343 3946.
E-mail address: p.ko@vanderbilt.edu (P.C. Ko).

http://dx.doi.org/10.1016/j.bandc.2014.07.009
0278-2626/

known neural mechanisms of priming. Early studies using functional magnetic resonance imaging (fMRI) found that behavioral priming to repeated objects was associated with reductions in neural activity, or *neural suppression* (Grill-Spector, Henson, & Martin, 2006). These studies showed that while item-specific priming elicited neural suppression in right ventral visual areas (i.e., the fusiform), category-wide priming elicited suppression in left ventral visual areas (Koutstaal et al., 2001; Simons, Koutstaal, Prince, Wagner, & Schacter, 2003; Vuilleumier, Henson, Driver, & Dolan, 2002). The location of these suppression effects suggested that the neural population representing an object becomes smaller and more selective, or *sharpened*, when re-activated upon viewing a repetition (Grill-Spector et al., 2006). The results of these studies also suggested that distinct item-specific and category-wide representations, residing in different hemispheres, were sharpened depending on whether a previously viewed object or an exemplar was confronted, an account consistent with a previous cognitive theory (Marsolek, 1999).

However, fMRI studies have also shown neural suppression in frontal areas related to priming, suggesting a mechanism distinct from the sharpening of a visual object representation (Dobbins, Schnyer, Verfaellie, & Schacter, 2004; Maccotta & Buckner, 2004; for a review, see Schacter, Wig, & Stevens, 2007). Unlike neural suppression found in the fusiform or early visual areas, the magnitude of neural suppression in frontal areas is correlated with the magnitude of behavioral priming, suggesting that it reflects the retrieval of stimulus–response mappings that were encoded during the first encounter with an object (Dobbins et al., 2004; Maccotta & Buckner, 2004). The encoding of these mappings could result in priming across stimulus changes, for example viewing one dog and reporting it as "living" could facilitate reporting a different dog as "living". We refer to this mechanism as the retrieval of stimulus–response mapping, or *S–R retrieval*.

Are these two neural mechanisms, sharpening and *S–R* retrieval, mutually exclusive routes to priming? Early cognitive studies suggested that these two mechanisms of priming run in parallel to each other. For example, Logan's (1990) model of priming demonstrated that both of these mechanisms are triggered and "race" to compete for output. Such a *parallel process hypothesis* could help account for the temporal differences between item-specific and category-wide priming. Although it is unlikely that viewing a repeated object or an exemplar necessitates that priming be strictly mediated by sharpening or *S–R* retrieval, respectively, viewing a repeated object may strongly favor the use of sharpening. Neural suppression in frontal areas that correlates with behavior, indicating the use of *S–R* retrieval, often require several presentations of a repeated object to be observed (Dobbins et al., 2004; Maccotta & Buckner, 2004), suggesting that *S–R* retrieval is not the "default" mechanism mediating item-specific priming. Likewise, viewing an exemplar may strongly favor the use of *S–R* retrieval. The visual discrepancy between two different dogs, for example, may result in bypassing the use of sharpening to generate priming. If item-specific priming favors the use of sharpening while category-wide priming favors the use of *S–R* retrieval, then it is possible that item-specific priming is faster than category-wide priming effects simply because sharpening is a faster process than *S–R* retrieval. In support of this account, a recent neuroimaging study recently showed distinct neural networks mediating item-specific and category-wide priming for scenes (Stevens et al., 2012).

Alternatively, both sharpening and *S–R* retrieval processes may always contribute to priming in discrete, sequential stages. This *serial stage hypothesis* can readily explain why item-specific priming is usually faster than category-wide priming. Both item-specific and category-wide priming involve an early perceptual stage followed by a late response stage of processing. While only item-specific priming involves more efficient processing of low-level perceptual features that were previously viewed, such as the specific orientations of lines in the picture, both item-specific and category-wide priming involve retrieval of previously encoded stimulus–response mappings. In support of this hypothesis, behavioral studies using additive factors logic have suggested that differences between item-specific and category-wide priming can be accounted for by early perceptual and later "post-perceptual" processing occurring in independent serial stages (Boehm & Sommer, 2012; Francis et al., 2008).

In the present study, we tested predictions of the parallel process hypothesis and serial stage hypothesis using ERPs. Our participants incidentally learned pictures of common objects and then performed a fragmented picture identification task while we recorded ERPs (Gollin, 1960). Items appearing in the identification task could be *Studied* pictures from the incidental study task, unstudied *Exemplar* pictures drawn from the same basic-level category as Studied items, or novel *Unstudied* pictures. We defined *item-specific priming* as faster behavioral responses to Studied items compared to Unstudied items, and *category-wide priming* as faster behavioral responses to Exemplar items compared to Unstudied items.

Based on previous research, we anticipated that Studied and Exemplar items would elicit less activity than Unstudied items, i.e., neural suppression. To help distinguish predictions of the opposing hypotheses, we focused on early- and late-stages of neural activity using stimulus- and response-locked ERPs, respectively. For early-stage activity, likely related to sharpening, both hypotheses can account for earlier neural suppression of Studied versus Unstudied items compared to neural suppression of Exemplar versus Unstudied items. The parallel process hypothesis interprets this pattern as differences in the timecourse of two different processes. The serial stage hypothesis interprets this pattern as facilitation to an early stage of processing in item-specific priming relative to category-wide priming. For late-stage activity, potentially related to *S–R* retrieval, the parallel process hypothesis predicts that only Exemplars would elicit changes relative to Unstudied items, while the serial stage hypothesis predicts that both Studied items and Exemplars should elicit changes in neural activity relative to Unstudied items relatively late in the time course. We anticipated difficulty in capturing this late stage activity with the traditional method of time-locked the ERP to a stimulus onset, since such processing could be masked by the temporal misalignment of response-based activity related to primed (Studied and Exemplar) and unprimed (Unstudied) items. Therefore, we examined response-locked ERPs to examine late stage activity (Horner & Henson, 2012).

We also conducted correlations between the magnitude of neural suppression and the size of behavioral priming effects. As previous studies have shown, such correlations are important evidence for *S–R* retrieval (Dobbins et al., 2004; Maccotta & Buckner, 2004). The parallel process hypothesis predicts that only category-wide behavioral priming would be significantly correlated with the degree of neural suppression that it evokes. In contrast, the serial stage hypothesis predicts that both item-specific and category-wide behavioral priming would be correlated with the degree of neural suppression that they each evoke.

2. Materials and methods

2.1. Participants

Participants were 24 right-handed native English speakers (18 female) with a mean education of 16.06 years (s = 1.61) and a mean age of 22.70 years (s = 1.45). All participants gave written informed consent and were paid $25/h. This study was approved by the Behavioral Science Committee of the Vanderbilt University Institutional Review Board.