



The ups and downs of repetition: Modulation of the perirhinal cortex by conceptual repetition predicts priming and long-term memory[☆]



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ABSTRACT

In order to better understand how concepts might be represented in the brain, we used a cross-modal conceptual priming paradigm to examine how repetition-related activity changes in the brain are related to conceptual priming. During scanning, subjects made natural/manmade judgments on a continuous stream of spoken nouns, written nouns and pictures of objects. Each stimulus either repeated in the same or a different modality with 1–4 intervening trials between repetitions. Behaviorally, participants showed significant perceptual and conceptual priming effects. The fMRI data showed that the conditions associated with the greatest behavioral priming exhibited the largest decreases in BOLD activity in left perirhinal cortex (PRc), as well as a few other regions. Furthermore, the PRc was the only region to show this relationship for the cross-modal conditions alone, where the concept but not the percept repeated. Conversely, repetition-related increases in PRc activity predicted better subsequent memory as assessed by a post-scan recognition test. These results suggest that repetition-related activity changes in the PRc are related both to the speed of access to a repeated concept and to that concept's later memorability.

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1. Introduction

The human brain has a remarkable ability to support internal representations of concepts irrespective of the modality of the perceptual sensory input. For example, the presentation of the word “guitar” can generate the same internal representation whether it was presented visually or aurally. Furthermore, conceptual representations are themselves multi-modal in the sense that we know not only what a guitar looks like, but also what it sounds like and what it feels like to hold one. While we can simply intuit the existence of conceptual representations, behavioral evidence for the existence of such representations comes from conceptual priming. Specifically, exposure to a concept can facilitate the subsequent processing of that same conceptual information, even when the repeated concept is presented in a different modality than the cue (Bassili, Smith, & MacLeod, 1989; Graf, Shimamura, & Squire, 1985; McClelland & Pring, 1991). Thus, the facilitation in response times observed during conceptual priming is not dependent on the repetition of the perceptual aspects of the presented stimuli, but rather on the conceptual similarity between the two presentations. While conceptual priming has long been

appreciated, the nature of the neural representation of conceptual information remains elusive.

There is emerging evidence that the perirhinal cortex (PRc), a brain region in the anterior portion of the medial temporal lobes, may contribute to the representation of conceptual information. Recent electrophysiological recordings in rodents demonstrate that the PRc has unique physiological properties that allow for the association of spatially disparate signals from multiple sensory cortices (Unal, Apergis-Schoute, & Pare, 2012). Furthermore, it is known that PRc receives auditory, visual and somatosensory unimodal inputs (Jones & Powell, 1970; Suzuki & Amaral, 1994), as well as polymodal cortical afferent projections from orbito-frontal cortex, dorsal superior temporal sulcus, cingulate cortex and posterior parahippocampal cortex (Suzuki & Amaral, 1994). Thus, existing anatomical and physiological data suggests that PRc can support the convergence and integration of featural representations that may contribute, at least in part, to a coherent conceptual representation.

To date, a few fMRI studies have reported results consistent with a role of the PRc in representing conceptual information. Taylor, Moss, Stamatakis, and Tyler (2006) found that PRc activation was sensitive to the congruency of two presented stimuli. Specifically, PRc activation was greater when a presented picture and sound were drawn from two different concepts (i.e. were incongruent) than when they were congruent (e.g. hearing a bark while seeing a picture of a dog). One interpretation of this finding

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is that in the incongruent condition, two concepts may be represented as compared to the congruent condition, where only one may be represented. Thus, PRC BOLD activity may track the number of concepts being considered. Similar results were reported by Haskins, Yonelinas, Quamme, and Ranganath (2008), where greater PRC activation was observed when a novel concept was being processed/learned. On a related note, a recent study by Wang, Lazzara, Ranganath, Knight, and Yonelinas (2010) found increased PRC activation during the encoding of words that were later produced during an exemplar generation task. Finally, O'Kane, Insler, and Wagner (2005) asked whether regions in the medial temporal lobes were sensitive to perceptual and conceptual repetitions. They found that repetition suppression in the left PRC was greater when the same task was performed with repeated words, relative to a new task. This suggests that the PRC representations were sensitive to the features of the items being accessed on each trial. These studies demonstrate that BOLD activation in PRC shows some relationship to conceptual processing, but is also sensitive to the specific features of a concept that are being accessed.

To expand on this literature, one complementary approach may be to leverage behavioral priming effects to identify brain regions that show sensitivity to conceptual repetition that is related to their behavioral facilitation. Voss, Hauner, and Paller (2009) recently utilized this approach in a perceptual priming paradigm. They demonstrated that repetition suppression in PRC during visual word presentation is correlated with the magnitude of behavioral priming across subjects. This study was the first to establish a relationship between measures of behavioral priming and repetition suppression in PRC. However, to our knowledge, this approach has not been applied to conceptual priming. Here, we adopted a similar approach to Voss and Paller and used a paradigm that allowed us to measure both perceptual and conceptual priming across different conditions. Sixteen subjects were presented with stimuli that repeated in either the same or a different modality within a span of 1–4 intervening trials. Each initial exposure could be a picture of an object, a written noun, or a spoken noun. Each repeated exposure could be any of these three modalities. To foreshadow the results, while other brain regions were sensitive to conceptual repetitions, the PRC emerged as the one region showing the most robust and consistent relationship with behavioral measures of priming. In addition, repetition-related enhancements in PRC activation were related to subsequent memory. Thus, we believe these data strengthen the evidence in favor of the PRC as being part of a network supporting conceptual representations.

2. Methods

2.1. Subjects. Sixteen (nine female) healthy, native English-speaking volunteers from New York University (NYU) participated in the study

All subjects gave informed written consent for the experiment in accordance with protocols approved by the University Committee on Activities Involving Human Subjects at NYU.

2.2. Stimuli. We presented 285 items (234 objects, 51 scenes) twice each

Scenes were included to help in localizing object and scene specific regions of cortex. While scenes were always presented as full color photographs (IMSI MasterClips[®] and MasterPhotos[™] Premium Image Collection, 1895 Francisco Blvd., East, San Rafael, CA 94901-5506, USA), objects could be presented in any of three modalities: spoken nouns, written nouns, and pictures of objects. Pictures were full color photographs collected from two online photography databases (www.photoobject.net; www.cepolina.com).

In a separate phase, a different cohort of participants was presented the photographs and instructed to label each with the first word that came to mind. Only photographs that received the same label across 80% of participants were included in the present study. Furthermore, these labels were in turn the basis of the spoken and written noun stimuli. Spoken nouns were presented using .wav files collected from the LDC American English Spoken Lexicon (<http://www ldc.upenn.edu/cgi-bin/aesl/aesl>). Object stimuli were grouped into 9 sets of 26 items each. Each set was presented in 1 of the 9 repetition conditions, and the exact mapping was counterbalanced across subjects.

2.3. Task

While scanning, participants were instructed to indicate, by making a button press as quickly as possible, whether the presented item was natural or manmade (Fig. 1). Items were presented in a continuous stream with a jittered inter-trial interval. Pictures and written nouns were presented for a fixed duration of .25 s while spoken nouns varied from .5 to 1 s. Initial trial presentations could be pictures of objects, written nouns and spoken nouns. Item repetitions could be in any of these three modalities. Thus, 1/3 of the time, the trial would repeat identically and 2/3 of the time the concept would switch modalities. Repetitions were separated by 1–4 (mean 2.5) intervening trials. During jittered inter-trial intervals (Dale, 1999), participants were instructed to fixate on a blue fixation cross which flashed green at the onset of each trial. There were a total of three within-modal conditions (SS—spoken nouns preceded by spoken nouns, PP—pictures preceded by pictures, WW—written nouns preceded by written nouns) and 6 cross-modal conditions (PS—spoken nouns preceded by pictures, WS—spoken nouns preceded by written nouns, SP—pictures preceded by spoken nouns, WP—pictures preceded by written nouns, PW—written nouns preceded by pictures, SW—written nouns preceded by spoken nouns). Throughout the paper, first presentations of items are referred to by a single letter (P, S or W) while repeated presentations are referred to by two letters where the first letter indicates the modality of the first presentation and the second letter indicates the modality of the repeated item presentation (e.g. PP or PW). After scanning, we administered a test assessing subsequent memory for all concepts. Subjects were presented with 234 old stimuli (26 trials from each condition) and 120 new stimuli, and asked to indicate their memory confidence on a scale from 1 (highly confident the item was studied) to 6 (highly confident the item was new). This test was self-paced. Importantly, all stimuli were presented as written words.

2.4. Imaging parameters

Imaging data were collected with a 3 T Siemens Allegra scanner. We acquired whole-brain functional data using an echoplanar imaging sequence across three scans each containing 297 volumes (TR=2000 ms, TE=30 ms, flip angle=85, 35 slices, 3 × 3 × 3 mm voxels, 20% distance factor) using coronal slices angled perpendicular to the long axis of the hippocampus. Because of this slice orientation, data from the most posterior parts of visual cortex were not collected. The first four volumes, collected for stabilization purposes, were discarded. A high-resolution, T1-weighted, full brain, anatomical scan (magnetization-prepared rapid-acquisition gradient echo; MPRAGE) was collected for visualization and registration.

2.5. Imaging preprocessing and registration

Preprocessing and analysis of fMRI data was conducted using FSL (version 4.1.9, <http://www.fmrib.ox.ac.uk/fsl/>) as well as custom Matlab (version 2010A, <http://www.mathworks.com/products/matlab/>) scripts. First, the data were motion corrected using

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