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Active retrieval facilitates across-episode binding by modulating the content of memory

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ABSTRACT

The contents of memory can be updated when information from the current episode is bound with content retrieved from previous episodes. Little is known regarding factors that determine the memory content that is subject to this across-episode binding. We tested whether across-episode binding preferentially occurs for memory content that is currently "active" and identified relevant neural correlates. After studying objects at specific locations on scene backgrounds, subjects performed one of two retrieval tasks for the objects on different scene backgrounds. In an active condition, subjects recalled object locations, whereas subjects merely dragged objects to predetermined locations in a passive condition. Immediately following each object-location retrieval event, a novel face appeared on a blank screen. We hypothesized that the original episode content would be active in memory during face encoding in the active condition, but not in the passive condition (despite seeing the same content in both conditions). A ramification of the active condition would thus be preferential binding of original episode content to novel faces, with no such across-episode binding in the passive condition. Indeed, memory for faces was better when tested on the original background scenes in the active relative to passive condition, indicating that original episode content was bound with the active condition faces, whereas this occurred to a lesser extent for the passive condition faces. Likewise, early-onset negative ERP effects reflected binding of the face to the original episode content in the active but not the passive condition. In contrast, binding in the passive condition occurred only when faces were physically displayed on the original scenes during recognition testing, and a very similar early-onset negative ERP effect signaled binding in this condition. ERP correlates of binding were thus similar for across-episode and within-episode binding (and were distinct from other encoding and retrieval ERP signals in both cases), indicating that active retrieval modulated when binding occurred, not the nature of the binding process per se. These results suggest that active retrieval promotes binding of new information with contents of memory, whereas without active retrieval, these unrelated pieces of information might be bound only when they are physically paired.

1. Introduction

Binding arbitrarily paired items experienced together during episodes is a central process in many accounts of memory (Underwood, 1969), particularly those of relational memory processing (e.g. Bunsey & Eichenbaum, 1996; Ryan, Althoff, Whitlow, & Cohen, 2000; Eichenbaum & Cohen, 2001; Preston, Shrager, Dudukovic, & Gabrieli, 2004; Prince, Daselaar, & Cabeza, 2005; Ranganath, 2010; Olsen, Moses, Riggs, & Ryan, 2012; Watson, Voss, Warren, Tranel, & Cohen, 2013). Most accounts of binding consider relations among items that co-occur within a spatiotemporal episode. However, it is possible that similar binding mechanisms support updating of memory for previous episodes by linking new information with existing memory content (Bunsey & Eichenbaum, 1996; Zeithamova & Preston, 2010). Although little is known regarding specific factors that influence binding across old and new episodes, some selection factor likely influences binding, such that not all memory content is bound with information in the current episode. One important selection factor could be the extent to which memory content is currently active due to a recent retrieval event (Nader, 2003). Active retrieval relative to passive re-exposure to memory content could be a particularly salient selection factor that determines the memory content subject to binding with new episodic information. That is,

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a targeted memory may be reactivated during active retrieval, but not necessarily during passive re-exposure to the same memory content. For example, we recently demonstrated that active retrieval systematically modulated the contents of memory that were currently active and bound with associatively novel information (Bridge & Voss, 2014).

At least two factors could influence which contents of memory become active: recent encoding or recent reactivation (Lewis, 1979). Binding over short time intervals may occur because recently encountered information stays active in memory for a brief period of time. Thus, as new information is encountered, it is bound to the temporally proximal information. Indeed, items presented in a temporally contiguous sequence are often better remembered later together (Schwartz, Howard, Jing, & Kahana, 2005; Sederberg, Miller, Howard, & Kahana, 2010). Moreover, neural activity reflects the reinstatement of the original temporal context (Turk-Browne, Simon, & Sederberg, 2012), suggesting that items presented close together in time are bound during learning (Briggs, Fitz, & Riccio, 2007). Retrieval may also influence what information is currently active (Briggs & Riccio, 2008). In this case, an old memory becomes active in memory, providing a means by which new information can be integrated into existing representations (Iordanova, Good, & Honey, 2011). Taken together, temporal contiguity may promote encoding of newly encountered information, whereas retrieval may promote updating of existing memories with new information. In both cases, information that is currently active in memory is bound with new information.

We hypothesized that the active engagement of retrieval modulates the extent to which binding between existing representations and new information occurs during learning (across-episode binding). This is because active retrieval could promote reactivation of old representations during encoding of new information, thereby enabling binding. Importantly, we hypothesized that binding would occur between new information that was physically present and old information that was only available in memory. On the other hand, we hypothesized that in the absence of active retrieval during learning, new information would be bound to old information only when these two pieces of information were physically paired during a subsequent test (within-episode binding). Importantly, we use binding to refer to the encoding of the association between two arbitrarily paired episodic elements, in this case a face with a specific object-location-scene context.

We manipulated the engagement of active retrieval processing just prior to encoding novel information. During the Study phase, subjects studied objects in locations on a scene background (original context scene). Then subjects completed a Refresh phase. During Active Refresh, subjects were presented with the objects and asked to actively recall the associated locations. In contrast, during Passive Refresh, subjects moved the objects to predetermined locations. Memory content was thus encountered in both the Active and Passive conditions; however, the extent to which active retrieval processes were engaged varied across conditions. Importantly, in both conditions, the old objects were presented on new scene backgrounds relative to the original study episode, and so original contextual information was not physically present. Furthermore, the same context scene background remained constant throughout each phase; however, the specific object-location information differed on each trial. Immediately following each Active and Passive trial, an unfamiliar face was shown, thus providing new information that could be bound with memory content (i.e. with the original object-location scene association). Face memory was tested in the final phase of the experiment, using either the original or new scene backgrounds. We hypothesized that faces would be preferentially bound to original memory content in the Active condition, thereby yielding better face memory relative to the Passive condition when tested with the original background.

We hypothesized that event-related potentials (ERPs) during face encoding in the Active condition would index across-episode binding between the new faces and the old, reactivated memory content. On the other hand, we hypothesized that ERPs during recognition in the Passive condition would index within-episode binding between the faces and the original memory content when they were physically paired during testing. Importantly, we were able to compare ERPs related to binding to ERPs related to other encoding and retrieval processes by comparing across the Active and Passive conditions. To the extent that similar binding processes were operative for the Active condition during encoding (across-episode binding) and for the Passive condition during recognition (within-episode binding), we expected similarities between these conditions in binding-related ERP correlates.

2. Methods

2.1. Subjects

Data were collected from 24 people (16 women; ages 18–33 years, $M=23$). Two subjects were excluded from all analysis due to failure to follow task instructions, leaving data from 22 subjects for analysis (21 were right handed). All subjects reported no history of neurological or psychiatric conditions and no current use of any psychoactive drugs. Written informed consent was obtained from all subjects prior to participation in accordance with the Northwestern University Institutional Review Board. Subjects were paid for their participation.

2.2. Stimuli

A set of 168 images of real-life objects was used (Brodeur, Dionne-Dostie, Montreuil, & Lepage, 2010). Each object was encapsulated by a white box with dimensions of $4.06 \times 4.06\ cm^2$. Eight photographs depicting real-life scenes were used as the background context images (from Hannula, Federmeier, and Cohen (2006)). The screen resolution was 1920×1080 pixels, which occupied $52 \times 29.25\ cm^2$ on an LCD monitor. The refresh rate was 60 Hz. Each object was presented with a red dot marking its center, which could be anywhere such that the whole object was visible on the background. Thus, objects could appear anywhere within the central $46.59 \times 22.75\ cm^2$ area of the screen. A set of 392 nonfamous faces was used (half male, half female; Althoff & Cohen, 1999). Face dimensions during Refresh (face encoding) were $16.25 \times 16.25\ cm^2$ and face dimensions during Recognition were $4.06 \times 4.06\ cm^2$.

2.3. Procedure

Each block was comprised of three phases, Study, Refresh, and Recognition (Fig. 1), each separated by a two-minute distractor task. There were four blocks, two with an Active Refresh phase and two with a Passive Refresh phase. Two scene background images were used in each block (one for Remote Context and one for Proximal Context), with a total of 8 different scenes in the experiment. The distractor task separating each phase involved configuring different block-shapes as they fell from the top of the screen, with the aim of forming complete rows of the block-shapes without any empty spaces (Pfister, 2008).

2.3.1. Study

During Study, subjects viewed objects presented at random locations on a scene background image. The scene background remained on the screen throughout the Study phase as objects were individually presented at randomized locations. A spatial location and scene background combination was thus uniquely tied to each object. We collectively refer to the object-location and Study background scene as the Remote Context (because it was remote relative to face encoding).

There were 42 study trials per block. Subjects were instructed to try to remember each object-location, as they would be given a test on the object locations later during Refresh. A 1000 ms fixation cross preceded each study trial. Then, an object appeared in a random location on the Remote Context scene for 3000 ms.

2.3.2. Refresh

In the second phase of the experiment, subjects completed object Refresh and face encoding. For each trial, subjects were prompted to move an object to a new location. A different scene provided the background during object-location Refresh.