Original Articles

Post-encoding control of working memory enhances processing of relevant information in rhesus monkeys (*Macaca mulatta*)

Ryan J. Brady*, Robert R. Hampton

Department of Psychology, Emory University, 36 Eagle Row, Atlanta, GA 30322, United States
Yerkes National Primate Research Center, 954 Gatewood Rd NE, Atlanta, GA 30329, United States

ARTICLE INFO

ABSTRACT

Working memory is a system by which a limited amount of information can be kept available for processing after the cessation of sensory input. Because working memory resources are limited, it is adaptive to focus processing on the most relevant information. We used a retro-cue paradigm to determine the extent to which monkey working memory possesses control mechanisms that focus processing on the most relevant representations. Monkeys saw a sample array of images, and shortly after the array disappeared, they were visually cued to a location that had been occupied by one of the sample images. The cue indicated which image should be remembered for the upcoming recognition test. By determining whether the monkeys were more accurate and quicker to respond to cued images compared to un-cued images, we tested the hypothesis that monkey working memory focuses processing on relevant information. We found a memory benefit for the cued image in terms of accuracy and retrieval speed with a memory load of two images. With a memory load of three images, we found a benefit in retrieval speed but only after shortening the onset latency of the retro-cue. Our results demonstrate previously unknown flexibility in the cognitive control of memory in monkeys, suggesting that control mechanisms in working memory likely evolved in a common ancestor of humans and monkeys more than 32 million years ago. Future work should be aimed at understanding the interaction between memory load and the ability to control memory resources, and the role of working memory control in generating differences in cognitive capacity among primates.

1. Introduction

Working memory is a central component of complex human cognitive abilities such as learning, language comprehension, planning, and reasoning (Unsworth & Robison, 2014). It allows for a limited amount of information to be kept available for processing in the absence of sustained sensory input, and the proficiency with which individuals do so is positively correlated with individual differences in scores of fluid intelligence (Baddeley & Hitch, 1974; McElree, 2006; Smith, Jonides, & Koeppe, 1996; Unsworth & Engle, 2007). Because the capacity of working memory is so limited, and because the relevance of information in working memory may change from moment to moment, it is critical to allocate working memory resources so as to process representations that are most relevant for current behavior (Chun, Golomb, & Turk-Browne, 2011; Cowan, 2010; Unsworth & Engle, 2007; Myers, Stokes, & Nobre, 2017). For instance, imagine an organism that has just encoded the spatial location of several food items varying in value. If a higher ranking individual approaches to take the highest value food, the lower ranking individual might benefit by allocating

working memory resources to the maintenance and retrieval of the lower-value food items. Thus, the control of working memory resource allocation is adaptive because it increases the utility of working memory.

Human working memory possesses control mechanisms that allocate resources to processing relevant information (Astle & Scerif, 2011; Berryhill, Richmond, Shay, & Olson, 2012; Griffin & Nobre, 2003; Lepsien, Griffin, Devlin, & Nobre, 2005; MacLeod, 1998; Matsukura, Luck, & Vecera, 2007; Sligte, Scholte, & Lamme, 2008), but it is unclear whether nonhuman primate working memory includes similar cognitive control. Because working memory is critical to complex cognitive functions in humans, it is possible that differences in the extent to which humans and nonhuman primates control working memory resources efficiently may explain quantitative and qualitative differences in cognition among primates. For instance, a lack of control over memory resources may result in a working memory system cluttered with irrelevant information, reducing the quality and quantity of information available to control behavior. We assessed whether or not monkey working memory possesses control mechanisms that allow for

relevant representations to recieve enhanced processing relative to other representations concurrently in working memory.

Both physiological (Fuster, 1997; Goldman-Rakic, 1995; Miller, Erickson, & Desimone, 1996) and behavioral (Basile & Hampton, 2010, 2013a; Tu & Hampton, 2014) evidence indicates that monkeys engage in short-term maintenance of representations relevant to current behavioral demands. Maintenance of some memories in monkeys is sensitive to competing cognitive load, indicating an active and cognitively demanding process akin to human working memory (Basile & Hampton, 2013a, 2013b). Processes supporting active maintenance in human working memory are thought to be greatly facilitated by verbal mechanisms (Baddeley, 2003; Wright et al., 1990), thus these findings are particularly striking because they suggest qualitative similarity in monkey working memory even in the absence of language.

Directed forgetting paradigms have been used to investigate human working memory control (Bjork & Woodward, 1973; MacLeod, 1998; Sheard & MacLeod, 2005) and have also been modified for use with pigeons (Kendrick, Rilling, & Stonebraker, 1981; Zentall, Roper, & Sherburne, 1995) and monkeys (Roberts, Mazmanian, & Kraemer, 1984; Tu & Hampton, 2014; Washburn & Astur, 1998). Subjects study a sample and a subsequent cue "instructs" them to either remember or forget the studied sample. Nonhuman animals, like humans, often show superior memory following remember cues, indicative of an active working memory control process. However, these findings from non-humans have been extensively critiqued and may be subject to alternative explanations such as motivational differences from unequal reinforcement on remember and forget trials (see Washburn & Astur, 1998; Zentall et al., 1995). A recent study in monkeys addressed many of these alternative explanations and still found evidence for active control in working memory (Tu & Hampton, 2014). Across several experiments controlling for reward expectation, differential reinforcement, the surprising nature of the probes, and the repeated use of a test following a forget cue, accuracy was significantly lower on memory tests following a forget-cue compared to a remember-cue (Tu & Hampton, 2014). These results extend the findings that monkeys engage in active maintenance (Basile & Hampton, 2013a, 2013b), and suggest that the engagement of this process can be under the control of external stimuli that differentiate between occasions on which memory is or is not beneficial.

After encoding a set of representations, behavioral demands may change, making some representations irrelevant. Working memory efficiency would be enhanced if resources were shifted to focus processing only on relevant representations. The directed forgetting paradigms used with monkeys thus far have not tested whether or not the target of working memory processing can be shifted among representations concurrently in working memory. For instance, the remember-cue used in Tu and Hampton (2014) indicated that *all* studied items should be remembered, and the forget-cue indicated that *none* of the studied items should be remembered. Thus, a fundamental question that has not been addressed is whether control mechanisms exist in monkey working memory that selectively allocate resources to the processing of relevant representations over other representations concurrently in working memory. To address this question we used a retro-cue paradigm in which a post-encoding cue identifies a single representation as most relevant among multiple representations encoded into working memory.

Retro-cue paradigms have been used in humans to investigate the ability to shift the target of processing in working memory (Aslte, Summerfield, Griffin, & Nobre, 2003; Astle & Scerif, 2011; Berryhill et al., 2012; Griffin & Nobre, 2003; Lepsien et al., 2005; Matsukura et al., 2007; Sligte et al., 2008). Participants were briefly presented with an array of stimuli to encode, and after the offset of the stimuli, a spatial cue indicated to participants which of the stimuli in the previously viewed array would be tested in an upcoming recognition test. Focused processing of the cued item is inferred when participants are either more accurate or respond more quickly on trials in which the cue

correctly predicts which item will be tested, compared to trials in which the cue incorrectly predicts which item will be tested, or to neutral trials that do not contain a cue (Astle & Scerif, 2011; Griffin & Nobre, 2003). Similar to the way in which a pre-cue shifts attention to enhance processing of stimuli in the environment (Posner, 2016), the retro-cue is thought to shift attention within working memory to the target item, enhancing the processing of that item, commonly referred to as the *retro-cue benefit* (Lepsien et al., 2005; Oberauer, 2013).

The two most prominent accounts of how retro-cues cause memory enhancement are the *prioritization* account and the *protection* account. The prioritization account maintains that the retro-cue focuses an "attentional spotlight" within working memory to guide the retrieval processes initiated at test (Griffin & Nobre, 2003; Rerko, Souza, & Oberauer, 2014). This shift in attention is most closely associated with faster reaction times to cued items compared to un-cued items, although initiating memory search with the target item could also improve accuracy. By contrast, the *protection* account posits that a shift in attention to the cued item draws memory resources away from the un-cued representations during the retention interval (Astle, Summerfield, Griffin, & Nobre, 2012; Makovski, Sussman, & Jiang, 2008). The protection account is most closely associated with improved accuracy for the cue item, rather than shorter response latency, but of course, enhancing discriminability of the target item in memory could also speed responding. These two accounts are therefore not mutually exclusive as improvements in latency or reaction time are consistent with both accounts, and may overlap with other explanations of the retro-cue effect (see Souza & Oberauer, 2016).

Although the exact processes invoked by retro-cues are still debated, it is agreed that shifting attention within working memory is a type of cognitive control (Berryhill et al., 2012). Thus, if we observe retro-cue effects in monkeys, this would indicate a previously unknown form of cognitive control in monkeys. The mechanism responsible for enhancing processing of retro-cued items appears to be visual-spatial rather than sub-vocal because the same results are obtained when participants are given a concurrent articulatory suppression task, (Makovski, Jiang, & Shim, 2006). Therefore, the retro-cue paradigm is well-suited for investigating control mechanisms within working memory in monkeys, particularly the specificity with which memory resources can be allocated after encoding multiple representations. Accordingly, we presented monkeys with stimulus arrays varying in cognitive load, and tested whether or not a retro-cue would result in enhanced accuracy, reaction time, or both, for the cued image.

2. Experiment 1

In Experiment 1, we tested whether memory would be enhanced by a spatial retro-cue that predicted which of two studied images would appear in a subsequent recognition memory test. Monkeys were trained on a yes/no recognition paradigm. During the study phase, an array of two images was presented, and during the test phase, monkeys had to decide whether a single test image had been present in the previously studied array. Half of the trials were *match* trials in which one of the studied images was presented at test, and half of the trials were *non-match* trials in which a non-studied image was presented at test. Between the offset of the study phase and the onset of the test phase, a retro-cue appeared in the location that had been occupied by one of the studied images. Match trials consisted of two types, congruent-match trials, and infrequent incongruent-match probe trials. Congruent-match trials were match trials in which the studied image previously in the cued location was tested. On incongruent-match probe trials, the image in the location other than the one indicated by the retro-cue was presented at test (Fig. 1). Changes in task difficulty can be reflected in changes in either accuracy or response time (Basile & Hampton, 2013b; Hanks, Kiani, & Shadlen, 2014). Subjects may respond slowly to maintain accuracy, or accept deterioration of accuracy while holding response latency relatively constant. Thus, changes in memory