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Dissociation of active working memory and passive recognition in rhesus monkeys



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ABSTRACT

Active cognitive control of working memory is central in most human memory models, but behavioral evidence for such control in nonhuman primates is absent and neurophysiological evidence, while suggestive, is indirect. We present behavioral evidence that monkey memory for familiar images is under active cognitive control. Concurrent cognitive demands during the memory delay impaired matching-to-sample performance for familiar images in a demand-dependent manner, indicating that maintaining these images in memory taxed limited cognitive resources. Performance with unfamiliar images was unaffected, dissociating active from passive memory processes. Active cognitive control of memory in monkeys demonstrates that language is unnecessary for active memory maintenance.

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1. Introduction

Human working memory can be compared to the display on an airport X-ray machine. Only a few bags can be viewed simultaneously and images of new baggage displace older images unless an operator exerts active control to freeze or manipulate the current view. Current models of human working memory differ in many aspects, but agree that the defining characteristic of working memory is active cognitive control (e.g., Baddeley, 2003; Cowan, 2008). Information is rapidly lost unless actively maintained, such as by verbal rehearsal in a “phonological loop” (Baddeley, 2003). Because maintenance by top-down cognitive control consumes limited resources, cognitive operations that compete for these resources cause forgetting in a demand-dependent manner. For example, the comparatively difficult task of deciding whether two abstract shapes are identical impairs memory performance more than does passively viewing the same shapes (Logie, 1986). Adding numbers impairs memory performance more than passively viewing num-

bers (Phillips & Christie, 1977). Cognitive control over working memory is likely a major factor in general intelligence (Unsworth & Engle, 2007), and may account for many cognitive differences between humans and nonhumans (Wynn & Coolidge, 2004). Thus, cognitive control is a critical and defining feature of human working memory.

Researchers have made substantial progress characterizing the capacity (Elmore et al., 2011; Heyselaar, Johnston, & Pare, 2011) and neural substrates (Constantinidis, Franowicz, & Goldman-Rakic, 2001; Fuster & Alexander, 1971; Heuer & Bachevalier, 2011; Miller, Erickson, & Desimone, 1996) of short-term memory in nonhuman primates. But it is unclear whether these studies characterize a cognitively-controlled system similar to human working memory (Washburn & Astur, 1998). The definitions of working memory in humans and nonhumans often differ. In the human literature, definitions of working memory focus on cognitive control (Baddeley, 2003; Cowan, 2008). In the nonhuman literature, working memory is often operationalized as memory relevant only to the current trial, as opposed to reference memory for the rules of the task (Shettleworth, 1998, chap. 6). Other criteria for identifying working memory can also lead to confusion. For example, working memory is not equivalent to short-term memory

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(Jenison & Squire, 2012). Humans can use working memory over relatively long delays if rehearsal is not interrupted (Milner, 1970), and short-delay memory tasks can require long-term memory if the amount of to-be-remembered information exceeds working memory capacity (Hannula, Tranel, & Cohen, 2006; Jenison, Mauldin, Hopkins, & Squire, 2011). Additionally, localized brain activity should not be uncritically equated with specific cognitive processes (Uttal, 2001). Cells in the prefrontal cortex of monkeys fire when monkeys view to-be-remembered images and continue to fire during the memory interval (Constantinidis et al., 2001; Fuster & Alexander, 1971; Miller et al., 1996). It is tempting to equate this monkey neural activity with human working memory based on fMRI studies that find activation of prefrontal cortex associated with active working memory in humans (D'Esposito, Postle, Ballard, & Lease, 1999; Stern, Sherman, Kirchoff, & Hasselmo, 2001). But this equation ignores the potential for cognitive differences between species. It is possible that monkeys and humans remember information differently even when performance or neural activity is superficially similar. For example, the inference of active working memory based on prefrontal activity is empirically contradicted by the fact that prefrontal activity is also found in experimentally naïve monkeys during passive viewing of images (Meyer, Qi, & Constantinidis, 2007). Resolving these ambiguities will require more definitive behavioral methods for assessing cognitive control in monkey working memory.

Surprisingly, there is no strong behavioral evidence for cognitively-demanding memory maintenance in monkeys. In humans, memory performance is impaired by performing a distractor task and more cognitively-demanding distractor tasks produce more impairment (Logie, 1986; Phillips & Christie, 1977), demonstrating that working memory requires limited cognitive resources. In monkeys, distractors presented during the memory interval, such as flashing lights (Prendergast et al., 1998), irrelevant images (Miller & Desimone, 1993; Miller et al., 1996), or a motor task (Washburn & Astur, 1998), can impair memory performance. However, unlike the case in humans, distractor tasks that required sustained activity and attention produced no more impairment than ones that only required passive viewing (Washburn & Astur, 1998). This indicates that the performance impairment in monkeys caused by these distractors was due to passive displacement of information rather than by competition for limited cognitive resources used to maintain information in working memory. Related investigations have tested for active control of memory in monkeys using directed forgetting paradigms or by providing opportunities for “rehearsal” of studied images. In humans, these approaches demonstrate cognitive control (Hourihan, Ozubko, & Macleod, 2009; Wright et al., 1990), but in monkeys they have not (Cook, Wright, & Sands, 1991; Washburn & Astur, 1998).

Previous tests may not have found evidence for active memory maintenance in monkeys because of the limited range of conditions under which these tests were conducted. Not all types of memory require active maintenance. For example, familiarity alone can support accurate recognition performance in many memory tests. Familiarity codes only whether stimuli have been seen previously (Yonelinas,

2002), and is an automatic, effortless process (Jacoby, 1991). In humans, the ability to distinguish items based on familiarity is unaffected by reduction in cognitive control by secondary tasks (Yonelinas & Jacoby, 1994) or intoxication (Bisby, Leitz, Morgan, & Curran, 2010). By contrast, when familiarity alone cannot support accurate performance, these manipulations do impair memory (Bisby et al., 2010; Yonelinas & Jacoby, 1994). Accordingly, we gave monkeys two memory tests that differed in the extent to which they could be solved by familiarity alone. In tests using a small set of familiar, frequently-repeating images (hereafter, familiar images), target images from previous trials were reused as distractors in later trials. This made all images highly familiar and created a high level of interference among test images, presumably making it almost impossible to distinguish target images from distractors based on relative familiarity. We hypothesized that active maintenance of memory for the target image would be required in these tests. We also administered control tests using a large set of unfamiliar, infrequently-repeating images (hereafter, unfamiliar images) from which recently studied targets could easily be discriminated from distractors at test based on relative familiarity. Thus, the critical difference between the familiar and unfamiliar image sets was whether monkeys could discriminate studied images from unstudied images based on familiarity.

2. Experiment 1: Primary findings

We presented monkeys with visual matching-to-sample recognition tests on touchscreen computers and required them to complete one of three distractor tasks during the memory interval (Fig. 1). The three tasks required the same motor response but varied in cognitive demand: (1) touch a blue square that appeared in a randomly-selected corner of the screen (motor only), (2) touch a photograph that appeared in a randomly-selected corner of the screen (motor + image perception), or (3) classify a photograph as depicting a bird, fish, flower, or person by touching the appropriate symbol in one of the four corners of the screen (motor + image perception + classification). Touching a uniform blue square should require the least cognitive processing. Viewing unfamiliar photographs may elicit more cognitive processing than viewing a blue square because the photograph is more visually complex and presumably more interesting. Finally, classifying photographs should require the most cognitive processing because the monkeys had to accurately assign the images to one of four categories to proceed to the memory test. If remembering required active maintenance of the studied image during the memory interval, accuracy should be impaired least by the motor task and most by the classification task. Passive retention should be unaffected by these manipulations of concurrent cognitive demand.

2.1. Methods

2.1.1. Subjects and apparatus

Six adult, male rhesus monkeys (*Macaca mulatta*; mean age = 8.2 years) experienced in matching-to-sample and

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