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Dissociation of item and source memory in rhesus monkeys

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ABSTRACT

Source memory, or memory for the context in which a memory was formed, is a defining characteristic of human episodic memory and source memory errors are a debilitating symptom of memory dysfunction. Evidence for source memory in nonhuman primates is sparse despite considerable evidence for other types of sophisticated memory and the practical need for good models of episodic memory in nonhuman primates. A previous study showed that rhesus monkeys confused the identity of a monkey they saw with a monkey they heard, but only after an extended memory delay. This suggests that they initially remembered the source – visual or auditory – of the information but forgot the source as time passed. Here, we present a monkey model of source memory that is based on this previous study. In each trial, monkeys studied two images, one that they simply viewed and touched and the other that they classified as a bird, fish, flower, or person. In a subsequent memory test, they were required to select the image from one source but avoid the other. With training, monkeys learned to suppress responding to images from the to-be-avoided source. After longer memory intervals, monkeys continued to show reliable item memory, discriminating studied images from distractors, but made many source memory errors. Monkeys discriminated source based on study method, not study order, providing preliminary evidence that our manipulation of retention interval caused errors due to source forgetting instead of source confusion. Finally, some monkeys learned to select remembered images from either source on cue, showing that they did indeed remember both items and both sources. This paradigm potentially provides a new model to study a critical aspect of episodic memory in nonhuman primates.

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1. Introduction

During his 1980 presidential campaign, Ronald Reagan often earnestly repeated the story of a World War II bomber pilot who heroically went down with his damaged plane rather than abandon an injured crewman (Berger, 2004). Although Reagan correctly remembered the story, he had forgotten its source: the 1944 Hollywood film *A Wing and a Prayer*. This example demonstrates the importance of remembering the source of information, and that source memory can be dissociated from item memory.

Source memory is a defining characteristic of human episodic memory (Tulving, 1993). Practically, source memory errors are a debilitating symptom of age-, injury-, or drug-related memory impairment (e.g., Cansino, 2009; Janowsky, Shimamura, & Squire, 1989; Mcintyre & Craik, 1987; Morgan, Riccelli, Maitland, & Curran, 2004). Therefore, tests of source memory and source memory errors in nonhuman animals are of great interest because they will inform our understanding of the evolution of memory, and provide models for neuroscientific investigations (Crystal, 2016; Templer & Hampton, 2013).

To assess source memory in nonhuman subjects, we adopt an operational definition of source memory that is grounded in studies of human memory. In many studies of human source memory, subjects study words, images, or abstract shapes presented with one of two secondary characteristics (e.g., presented in different colors, in different screen locations, in different sensory modalities). At test, subjects demonstrate item memory by discriminating studied items from non-studied items, and demonstrate source memory by additionally discriminating among studied items based on the secondary study characteristic. In one common variant, subjects are tested in an "exclusion" condition (Jacoby, 1991, 1999), in which they are instructed to accept only previously studied items from one source, avoid previously studied items from the other source, and also avoid unstudied items. For example, subjects might study line drawings in different colors (e.g., a green fork, a red key), and then see a mix of studied and unstudied black drawings at test and be instructed to only accept items if they had been studied in red (Cycowicz, Friedman, & Snodgrass, 2001). In this

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example, item memory is operationalized as the ability to discriminate between studied and unstudied images (e.g., accept the key but reject a swan), and source memory is operationalized at the ability to discriminate between black test images based on the color they appeared in at study (e.g., accept the key and reject the fork).

Researchers studying source memory have used a wide variety of secondary study characteristics as the "source" of the item, including the item's color (Cycowicz et al., 2001; Kensinger & Corkin, 2003), the color of a surrounding box (Mollison & Curran, 2012), whether the item was read or heard (Jacoby, 1999), the gender of the speaker during auditory study (Bornstein & Lecompte, 1995; Senkfor & Van Petten, 1998), item location on a computer screen (Mollison & Curran, 2012; Slotnick, Moo, Segal, & Hart, 2003), or whether subjects were required to make a pleasant/unpleasant or a concrete/abstract judgement about the item during study (Dobbins, Foley, Schacter, & Wagner, 2002). What is common across the rich variation in the nature of "source" in these studies is that the measure of source memory has been consistently operationalized as the ability to discriminate between items with different secondary study characteristics during a later memory test.

Despite the importance of studying source memory in nonhuman animals, evidence that nonhumans remember the source of learned information is scarce. One proposed example comes from studies of rats (Crystal & Alford, 2014; Crystal, Alford, Zhou, & Hohmann, 2013). In these tests, rats remembered not only where they previously found food, but also whether they learned the location of the food by navigating there themselves or by being placed there by the experimenter. If the rat found chocolate itself, it could find more chocolate in the same location later. But if the rat was placed at a chocolate location by the experimenter, there would be no chocolate in that location later. Rats demonstrated source memory by re-visiting the chocolate locations they found themselves more often than the chocolate locations at which they were placed by the experimenter. Their source memory was dependent on the integrity of the hippocampal CA3 subfield, and the rats could be retroactively cued after study as to which source predicted replenishing chocolate. However, the degree to which finding or being carried to a food site instantiates "source" in the same way this term is used with humans is not settled. In addition, evidence of source memory in rats would imply that it is a common feature of mammalian memory and that it should also be found in species that are more closely related to humans such as other primates; however, demonstrations of source memory in nonhuman primates are surprisingly lacking.

A recent study of auditory-visual memory integration (Adachi & Hampton, 2011) suggested the existence of source memory, source memory errors, and a delay-dependent dissociation of item and source memory in rhesus monkeys. During the study phase of each trial, monkeys watched videos of known conspecifics. After a retention interval, they were required to select the image of the studied individual from among four other known individuals. Some retention intervals included a vocalization from one of the four to-be-avoided distractor monkeys. This setup parallels human source memory methods in which source is defined by whether studied items had been seen or heard, and subjects must follow an exclusion rule of only selecting studied items from one modality (e.g., Jacoby, 1999). When subject monkeys erred, they chose the picture of the monkey they had heard during the retention interval more often than expected by chance. However, they chose the heard monkey in error only when the vocalization occurred at the beginning of the retention interval, not when it occurred at the end of the retention interval (unpublished data). One interpretation of this finding is that monkeys remembered the identities of both the seen monkey and the heard monkey, and generally selected the seen monkey at test, as was required. However, after a long delay they sometimes forgot which monkey was seen and which heard, and erroneously chose the heard monkey at test due to a source memory error. That this only happened when both pieces of information were presented at the beginning of the retention interval, and not when the heard monkey was presented at the end of the retention interval, may indicate that source memory is forgotten more quickly, or confused more easily, than item memory under these conditions.

In this study, we evaluated the source memory interpretation of the pattern of findings from the previous study of cross-modal integration. Monkeys studied two color images that were learned in two different ways, by touching one and by classifying the other. Our paradigm is similar to previous studies of source memory in humans, in that subjects must remember items that were studied in two different ways. Our approach most closely parallels studies of source memory in humans in which source is defined by the judgment subjects were required to make about items at study (e.g., Dobbins et al., 2002). In Experiment 1a, monkeys earned food at test by selecting the touched image and avoiding both the classified image and two unstudied distractor images. Thus, this paradigm also employs an exclusion rule (e.g., Jacoby, 1991, 1999) in which subjects must select items from one source but not the other. In accord with our operational definition, item memory was evaluated as the ability, at test, to discriminate studied items from unstudied items, and source memory was evaluated as the ability to discriminate between studied items based on how they were studied.

As in the previous monkey study, the item from the to-be-avoided source occurred at the end of the retention interval. In Experiment 1b, we randomly intermixed probe trials on which both images were studied at the start of the retention interval, reproducing the conditions from the previous study under which monkeys made apparent source errors. The study by Adachi and Hampton (2011; and unpublished data) suggests a source memory hypothesis whereby monkeys initially encode both item and source information but source information decays more rapidly than item information. This hypothesis makes three predictions for this experiment: (1) in Experiment 1a, when memory for the to-be-avoided source is still strong during test, monkeys should be able to learn to avoid the classified image; (2) in Experiment 1b, when memory for both sources is weaker during test, they will increase choices of the classified image; (3) because item memory is still relatively strong, errors will not be to unstudied distractors but will be selective to items from the to-be-avoided source.

2. Experiment 1a: Acquisition of source memory discrimination

2.1. Methods

2.1.1. Subjects

We tested twelve adult male rhesus monkeys (mean age at start: 8.5 years) in their home cages. Whenever possible, monkeys were pair-housed when not testing. Pair-housed monkeys were separated during testing by a protected-contact divider (a plastic dividing wall with small holes) that allowed them limited visual, auditory, and tactile access to their partner but not their partner's computer screen. Monkeys received full food rations after each day's testing, and water was available ad lib. All monkeys had prior experience with touchscreen-based cognitive tasks including perceptual classifications and delayed matching of images (Basile & Hampton, 2013a, 2013b, 2013c). All testing complied with US law and the National Institutes of Health guide for the care and use of laboratory animals.

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