



The interaction between working and reference spatial memories in rats on a radial maze



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ABSTRACT

The interaction of reference and working memory was studied in rats on an eight-arm radial maze. Each trial involved a two-phase procedure in which a rat was forced to enter four arms on the maze in a study phase and then was allowed to choose among all eight arms in a test phase given 5-s later, with choice of only the previously unvisited arms rewarded. For each rat, two arms on the maze were designated as reference memory arms because they were never entered in the study phase and were always rewarded in the test phase. The other two arms never entered in the study phase and rewarded in the test phase were working memory arms and varied randomly from trial to trial. In Experiment 1, rats showed acquisition of equivalent preference for entering the reference and working memory arms in their first four choices of the test phase. Subsequent tests carried out in Experiment 2 compared performance at 5-s, 1-h, and 24-h retention intervals when reference memory and working memory were congruent and incongruent. Higher accuracy for choice of reference memory arms than working memory arms appeared at the 1-h and 24-h retention intervals on congruent tests but not on incongruent tests. A process dissociation procedure analysis indicated that working memory but not reference memory declined over the 24-h retention interval. The interaction of working and reference memory was shown by superior choice of reference memory arms on congruent tests than on incongruent tests at 1-h and 24-h retention intervals but not at the 5-s retention interval. These findings suggest that working and reference memory are independent systems that can facilitate and compete with one another.

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The proposition that there are multiple memory systems has become popular in both the human and nonhuman animal (hereafter referred to as animal) memory literatures. The invention of the radial maze for testing spatial memory in rats (Olton and Samuelson, 1976) led to experiments that particularly promoted the idea of different memory systems in rodents. On a radial maze consisting of 8–16 arms radiating from a central hub, selected arms were designated as working memory and reference memory arms (Olton and Papas, 1979). Reference memory arms were a subset of arms that never contained food reward, and a reference memory error was defined as entrance into any of these arms. The complementary set of arms on the maze was always baited with food at the beginning of a trial and was designated working memory arms. Initial visits to these baited arms were considered correct responses, but any revisits prior to collecting all of the rewards were defined as working memory errors. Because the nonbaited reference memory

arms were always the same arms on every trial, reference memory was thought of as a long-term, permanent memory or habit (Honig, 1978). Because the pattern of visits to baited arms changed from one trial to another, rats had to remember a different set of arms on each trial. Thus, working memory was short-term and involved different information on each test trial.

In addition to these procedural and theoretical distinctions between working and reference memory, several lines of evidence suggested they might be controlled by different neural structures. For example, Olton and Papas (1979) found that hippocampal (fimbria-fornix) lesions markedly reduced the accuracy of working memory but had no effect on reference memory performance. Injection of a cholinergic neurotoxin into the hippocampus selectively impaired acquisition of spatial working memory but had no impact on the acquisition and retention of reference memory (Shen et al., 1996). Evidence for double dissociation between working and reference memory tasks and brain structures in rats has been reported (Packard et al., 1989; Packard and White, 1990). Separate groups of rats received lesions of the hippocampus (fimbria fornix) or the caudate nucleus. Fornix lesions produced a large increase in

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working memory errors relative to control rats but had no effect on the performance of a reference memory task that involved entering arms containing a light cue for reward. By contrast, caudate lesions, but not fornix lesions, produced a significant increase in reference memory errors. Finally, nicotine infusion significantly lowered working memory errors in rats on the radial maze but had no impact on reference memory errors (Levin et al., 1996).

An even greater number of memory systems have been postulated to underlie human memory. Arising from early experiments on short-term memory in people, it has been suggested that working memory in humans is a temporary storage system in which critical processing of information is carried out for long-term storage (Atkinson and Shiffrin, 1968). In one model of working memory (Baddeley, 1992), working memory consists of a central executive that controls and integrates information from slave systems consisting of a visuospatial sketch pad and a phonological loop. Theories of human long-term memory suggest that it consists of two major divisions, declarative and nondeclarative (Squire, 2004). Declarative memory is memory for facts and events and may further be divided into episodic or autobiographical memory for personal past experiences and semantic memory for general information (Tulving, 1985). Nondeclarative memory is said to be procedural and provides us with the ability to learn and remember various motor skills. A further important distinction often made between these types of memory is that declarative memory is explicit and conscious while nondeclarative memory is implicit, unconscious, and automatic. Finally, evidence from neurological studies suggests that formation and retention of declarative memories may reside in the medial temporal lobe and hippocampus, but that procedural nondeclarative memories may reside in basal ganglia structures (White et al., 2013).

The multiple memory systems framework has not gone unchallenged, with other theorists arguing that many of the phenomena that appear to argue for separate memory systems can be explained by properties of a single memory system (Berry et al., 2008; Shanks and Berry, 2012). In particular, Jacoby and his colleagues have suggested that measures of implicit or unconscious memory may be contaminated by explicit or conscious memory (Hay and Jacoby, 1996; Jacoby et al., 1992, 1993). That is, one can never be certain that awareness of material previously presented does not influence performance on tests of implicit memory.

To overcome this problem, Jacoby (1991) developed the *process dissociation procedure* (PDP). The PDP approach compares performance under a condition in which habit (implicit memory) and recollection (explicit memory) work in concert to show retention (Congruent condition) with performance under a condition in which habit and recollection are opposed to one another (Incongruent condition). For example, Hay and Jacoby (1986) had subjects memorize associatively related words (form habits), such as *knee-bend* and *knee-bone*, with *knee-bend* occurring more often than *knee-bone*. In a subsequent phase of the experiment, subjects were shown lists of word pairs that included either *knee-bend* (congruent) or *knee-bone* (incongruent). A final memory test presented word fragments (e.g., *knee-b-n-*), with subjects asked to complete the word fragment. In the congruent condition, habit and memory for the recently presented test list were the same. Thus, the probability of remembering the recently presented item (*knee-bend*) was the sum of the probability of remembering its recent presentation (R) plus the probability of *knee-bend* being elicited as a habit (H) on those occasions when the recent presentation of *knee-bend* was forgotten ($1 - R$). The complete equation for recollection of *knee-bend* under congruent testing is thus $R + H(1 - R)$. In the incongruent condition, however, *knee-bend* should only be remembered as a habit and thus its probability of being remembered is $H(1 - R)$.

By placing habit and intentional recollection in concert and in opposition, Hay and Jacoby (1996) were able to construct equations

for R and H. If the probability of recalling *knee-bend* as an automatic or unconscious habit was found in the incongruent condition, subtracting incongruent recall of this item from congruent recall of this item (Congruent – Incongruent) should yield a pure measure of R. Because the probability of recalling *knee-bend* as a habit in the incongruent condition is $H(1 - R)$, then $H = \text{Incongruent Probability} / (1 - R)$. Estimates of R and H were calculated from obtained data and suggested that habit and recollection were products of independent memory systems. Thus, varying the presentation rate of items in the final study phase affected R but had no effect on H. Conversely, varying the probability of items occurrence in the habit formation phase (*knee-bend* versus *knee-bone*) affected H but had no effect on R.

Recently, Tu and Hampton (2013) extended the PDP approach to the study of memory in rhesus monkeys. Monkeys were tested for working memory by presenting a single clip-art sample image on a screen. After a delay, four images were shown and a monkey was rewarded only for choosing the image that matched the sample. Habit was manipulated by presenting some sample-match pairs more often than others within quads of four test images. The results were strikingly similar to findings from human experiments, with R and H measures derived from the obtained matching-to-sample data showing independence of habit and memory. Thus, the H factor increased as the probability of a sample-match pair increased from 25% to 100%, but level of R remained unchanged. When the retention interval was lengthened, however, R scores decreased significantly but H scores were unchanged. An extension of these procedures found dissociation of memory systems based on brain lesions (Tu et al., 2011). Monkeys with perirhinal cortex removal showed a marked reduction in R (delayed matching) performance relative to normal control monkeys, but H scores were equivalent in both groups.

In the experiments reported here, we examined the possibility that independent but competing memory systems could be found in a nonprimate species, the rat. We first trained rats on a radial maze to remember a set of working memory (WM) arms that changed randomly from trial to trial and a set of reference memory (RM) arms that remained the same over trials (Experiment 1). The rats were then tested at different retention intervals under conditions in which WM and RM were congruent or incongruent (Experiment 2). The two goals of these experiments were (1) to test for the independence of WM and RM, and (2) to examine competition and interaction between WM and RM as the retention interval changed.

1. Experiment 1

Rats were trained using a win-shift procedure on an eight-arm radial maze. On each daily session, each rat was given an initial trial in the study phase in which it was forced to enter four arms on the maze, with a food reward at end of each arm. Rats could enter only the four selected arms because the doors leading to the four remaining arms were closed. On a test trial given immediately after the study trial, a rat was placed in the center of the maze with all eight arms open but with food placed at the ends of only the arms not entered in the study phase. A correct response was scored as an initial visit to any one of the rewarded (not previously entered) arms in the first four choices. Thus, a rat could make a perfect score of 100% by entering all four rewarded arms in the first four choices.

The novel manipulation used in this study was to arrange for each rat to have the same two arms correct on every test trial. These arms were thus defined as RM arms. For example, if arms 2 and 6 were RM arms for a given rat, those two arms would never be open in the study phase. The four arms visited in the study phase were chosen randomly from the remaining six arms on the maze. The two

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