Working Memory in Aged Rats

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The performances of young and aged rats were compared on a spatial (spatial delayed nonmatching-to-sample) and a nonspatial (object delayed nonmatching-to-sample) test of working memory. Although evidence was found that aging slowed acquisition of both of these tasks, performance over different retention intervals of up to 60 s was normal once the task was mastered. An impairment was found, however, in the performance of the spatial test when the number of locations to be remembered on each trial was increased from one to two. The conclusions of this study are that under some conditions, the retention capabilities of aged rats may not change and that some acquisition impairments do not reflect alterations in learning or memory per se, but, in common with other studies, deficits in the remembrance of spatial locations may be found.

In recent years, an increasing number of experiments have been performed to examine whether aging in animals produces consistent changes in learning and memory. Most of the studies on aged rats have concentrated on measuring the rate of learning or relearning tasks, whereas fewer studies have compared the rate at which acquired information is forgotten (Kubanis & Zornetzer, 1981). An obvious exception to this generalization is the one-trial passive avoidance task that some investigators have shown to be sensitive to aging in rats (Bartus, Dean, Goas, & Lippa, 1980; Brizee & Ordy, 1979; Kubanis & Zornetzer, 1981; Martinez & Rigter, 1983). That is, aged rats tend to make the inappropriate response, step down, for example, faster than young animals. This finding is often regarded as evidence of faster forgetting (Kubanis & Zornetzer, 1981; Martinez & Rigter, 1983).

Although the passive avoidance task has proved a useful tool in animal research, it does not appear to be comparable to tests of memory typically administered to people. Indeed, reports of amnesic patients who are able to make appropriate avoidance responses and yet report remembering nothing of the original learning experience (Clapared, 1911; Weiskrantz & Warrington, 1979) highlight the fact that this kind of task may be taxing memory mechanisms quite different from those usually tested in people (Mishkin & Petri, 1984).

Therefore, in this study, we used tasks that allow rates of acquisition and forgetting to be measured and that appear to be more comparable with those used with people. This feature was made possible with tests of object recognition (Experiment 1) and spatial recognition (Experiment 2) in which the information to be retained is only of value for one trial. Consequently, new information must be retained on each subsequent trial, and therefore animals can be tested repeatedly to determine forgetting curves for each animal. Such tasks have been described as tests of working memory (Honig, 1978; Olton, Becker, & Handelmann, 1979). This particular use of the term should, however, be distinguished from the slightly different notion of working memory as used in human cognitive psychology, where the term refers to a temporary store used for a wide range of cognitive activities (Baddeley, 1986; Baddeley & Hitch, 1974).

The tests used in this study have the same design as forced-choice recognition tasks given to people. The major differences are that the animals were not required to learn a list of items before recognition was tested and that the spatial recognition tasks (Experiments 2 and 3) repeatedly used the same stimuli (i.e., two arms of a maze), thereby taxing recency rather than recognition. Several studies have shown that aged monkeys (Presty, Cork, Price, Bachevalier, & Mishkin, 1984), patients with Alzheimer's disease (Albert & Moss, 1984), and patients with Korsakov's syndrome (Aggleton, Nicol, Huston, & Fairbairn, 1988) are impaired on similar tests of visual recognition, indicating that such tests may be valuable in assessing the effects of aging.

Experiment 1: Object Delayed Nonmatching to Sample

Rats of various ages were trained in a test of object recognition, delayed nonmatching to sample (Aggleton, 1983). The animals were tested in a Y maze in which the start box and the two goal boxes were removable. In each trial the start box matched one of the goal boxes and differed from the other. The rats were rewarded for selecting the goal box that differed from the start box (nonmatching). Because the start box and the goal boxes were changed after every trial, this task taxed working memory (Honig, 1978; Olton et al., 1979). In this and all subsequent experiments, male and female rats were used to determine the generality of the findings.

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Methods

Subjects. The subjects for this and the subsequent experiments were pigmented rats of the DA strain, none of which had undergone previous training. This strain was chosen because it has proved capable of readily learning the object recognition task (Aggleton, 1985). Furthermore, this inbred strain is not prone to obesity on an ad-lib diet, thereby helping comparability between groups, particularly by minimizing differences in motivation. The rats, which were derived from stock supplied by Bantin and Kingman (Hull, England), were bred and raised in the laboratory. The animals were reared in an isolated room within a conventional unit with 14:10-hr light/dark photoperiod. After weaning, the animals were kept in standard cages in groups of 3–5 and maintained ad libitum on chow (Labsure ERM) and water. Any animals that showed signs of ill health during regular monitoring were eliminated from the program. Under these housing conditions, the maximum life span of this strain has been approximately 26 months. None of the rats in this or the subsequent studies had been used for breeding.

Throughout the experiment, all animals were caged individually and fed approximately 15 g of laboratory diet daily so that their weights did not drop below 85% of normal body weight. The ages of the 8 young control rats (4 male and 4 female) at the outset of the experiment, which lasted 2–3 months, ranged from 3 to 5 months, whereas the ages of the 6 old male rats ranged from 17 to 20 months ($M = 18.3$) and those of the 6 old female rats ranged from 16 to 18 months ($M = 17$). The mean weights of the rats at the completion of the study were as follows: old males, 241 g; young males, 236 g; old females, 197 g; young females, 186 g.

Apparatus. Each arm of the aluminum Y maze (Figure 1, left) was 13 cm wide and 20 cm high. Fifty pairs of hardboard boxes served as start and goal boxes. These boxes fitted into the end of each arm of the maze, forming a total arm length of 26 cm. The appearance of the boxes constituting each pair was made as similar as possible, but each pair was distinct from every other pair. Specifically, the walls and floors of the boxes were painted in different colors and patterns, and the floors were lined with various materials, such as sandpaper, wooden strips, metal, Plexiglas, and cloth. In addition, each pair contained an identical object, such as a plastic cup, a metal bracket, or a wooden block, although no two pairs contained the same object. The floors of the boxes, which extended toward the center of the maze, began 8 cm from a Y-shaped aluminum guillotine door at the center of the Y maze (Figure 1, left). Food pellets (45 mg, Campden Instruments) could be dispensed under the back of each box. The Y maze was illuminated by a fluorescent ceiling light 215 cm above the apparatus. Further details of the apparatus have been published (Aggleton, 1985).

Procedure. After a two-week period of pretraining, which involved handling the rats daily and training them to run in the Y maze for food pellets, the experiment began. To start each test session, the rat was placed in an arm with a featureless start box. The central door was then raised, and the animal was allowed to choose between two arms that contained a matching pair of distinctive goal boxes ($A_1^+$ and $A_2^+$, Figure 1, left). The rat was deemed to have made a choice when all four paws entered an arm, whereupon the guillotine door was lowered. On this first run of the session, the animal was rewarded with three 45-mg food pellets (Campden Instruments) in whichever box it entered. The animal was confined to this box ($A_1^+$) for approximately 20 s, while the other two test boxes were replaced. The central door was then raised, revealing a familiar box ($A_1^-$) in one arm and a novel box ($B_1^+$) in the other (Figure 1, left, Panel II). The animal was rewarded with three food pellets if it entered the novel box.

After 20 s of confinement in Box $B_1^+$, the second trial began (Figure 1, left, Panel III). The central door was then raised, and the animal chose between the familiar appearance of Box $B_2^-$ and Novel Box $C_1^+$. This sequence was repeated with new pairs of boxes for a total of 10 trials, and selection of the novel box was always rewarded (Trial
Figure 2. Nonmatching-to-sample results. (Left: Performance over the first 200 acquisition trials of the nonmatching task. For animals that required less than 200 trials to reach criterion, the additional data have been taken from the 0-s delay condition. Right: Performance with delays of 0 or 60 s between stimulus presentation and recognition test. S.E. = standard error.)

Results

Figure 1 (right) shows the number of trials and the total number of errors, including correction trials, preceding the 80% criterion score. There were no differences between the male and female rats in either age cohort. Statistical comparisons between the acquisition performances of the young and old rats required to reach criterion used nonparametric statistics in response to the skew distribution of the scores. These analyses showed that the old rats (data for male and female rats combined) required significantly more trials to reach criterion than the young rats (Mann-Whitney n = 8, 12; U = 16.5; p < .01). Postmortem examination, however, revealed that both of the aged rats that failed to reach the criterion score had pituitary tumors. Nevertheless, when the results of these two animals were excluded, the young animals still acquired the task significantly faster than the remaining old animals (mean number of trials to criterion for old rats = 206 and for young rats = 144, U = 16.5, p < .05).

Figure 2 (left) shows the rate at which performance on the object recognition task improved over the first 200 trials. For animals that required fewer than 200 trials to reach criterion, we used the data from the 0-s delay condition, which immediately followed acquisition of the task and used the same testing procedure. The scores for the two animals with pituitary tumors were excluded. The young rats performed better than the aged rats, and this group difference was confirmed in an analysis of variance (ANOVA) comparing performance over the four blocks of 50 trials, F(1, 16) = 15.51, p < .01. Although there was a highly significant improvement over successive blocks of trials, F(3, 48) = 10.85, p < .001, there was no evidence of a significant interaction between the rates of learning of the young and aged rats (F < 1). That is, although both groups of rats improved at a similar rate, they started at different levels (Figure 2, left);
whereas the young rats showed the expected spontaneous preference for the novel (correct) object (Aggleton, 1985), the old rats required 100 trials before they started to show any clear preference for the novel stimuli.

The scores of the two groups over the 50 performance trials at 0-s (the same as the acquisition condition) and 60-s retention intervals are shown in Figure 2 (right). A three-way analysis comparing age, sex, and delay confirmed the expected decline in performance with the 60-s retention delay, $F(1, 12) = 22.87, p < .001$. There was, however, no overall effect of age ($F < 1$) or sex, $F(1, 12) = 1.59$. Although there was an indication that the scores of the aged rats fell faster with the increasing delay, this result was not significant, $F(1, 12) = 2.67$, and inspection of the scores showed it to be largely the effect of two rats that produced the highest scores on the 0-s condition but that performed poorly after 60 s. There was, however, evidence of a significant interaction between sex and delay, $F(1, 12) = 4.91, p < .05$, which reflected the finding that the performance of the male rats fell with time.

**Discussion**

The results showed that although old rats may be significantly slower than young rats to acquire a test of object recognition, the same animals are not necessarily impaired on the retention of individual stimuli. The major difference between the groups lies in the much higher initial preferences for the novel boxes shown by the young rats, rather than in the rates of learning (Figure 2, left). This finding is consistent with a recent study in which, on the basis of a single trial, evidence was presented that aged rats may show diminished exploration of a novel object but nevertheless appear able to discriminate its novelty (Willig et al., 1987).

The results from the second phase of Experiment 1 showed that once the task had been mastered, there were no differences between the young and aged groups, even when the retention delay was increased. Given the absence of a ceiling effect, the equal ability of the two groups to select the novel stimulus implies that the animals were equally able to discriminate and remember the appropriate test stimuli. This implication, in turn, strongly suggests that the initial acquisition deficit in the aged rats was the result of some factor other than sensory discriminability or learning ability per se. One possible explanation is that the performance of the aged rats reflects a difference in emotionality rather than learning.

This difference might alter the animals’ responsiveness to the test apparatus or the novel stimuli and thereby primarily affect the first few test sessions. Support for this proposal comes from reports that old rats take longer to adapt to new test apparatuses (Beatty, Bierley, & Boyd, 1985), are differentially affected by a lack of handling before a learning task (Doty, 1968), and show reduced duration of exploration of novel objects in spite of a normal ability to discriminate their novelty (Willig et al., 1987).

Much more persuasive evidence of a memory disturbance would have been provided by a deficit on the 60-s retention interval. Clearly, however, aging did not alter the degree of difficulty when the retention interval was increased after the task was mastered (Figure 2, right). To examine the generality of this finding, we decided to investigate the acquisition and subsequent performance of a spatial test of nonmatching to sample. In this experiment, each rat was required to remember which of two arms in a T maze it had been forced into on the previous information trial in order to alternate to make the correct choice. Because each pair of information and test trials was independent from the previous trial, this task taxed working memory. However, the stimuli, that is, the locations, were constantly repeated, and therefore this spatial test taxed recency judgements.

**Experiment 2: Spatial Delayed Nonmatching to Sample (T Maze)**

**Subjects.** The subjects were 22 rats of the DA strain. At the start of testing, there were 4 male and 4 female rats aged 2.5–3 months and 14 aged rats, which included 7 male rats (14–18.5 months old at the start of the experiment, $M = 17.4$) and 7 female rats (16–18.5 months old, $M = 17.2$). The experiment lasted for a further 2–3 months. The housing and feeding arrangements were as in the previous experiment. The mean weights of the rats at the completion of the study were as follows: old males, 294 g; young males, 201 g; old females, 210 g; young females, 182 g.

**Apparatus.** The floors of the T maze were 10 cm wide and made of aluminum. The stem of the maze was 80 cm long, with a guillotine door located 33 cm from the beginning. The crosspiece was 136 cm long, and at each end there was a food well 4 cm in diameter and 0.75 cm deep. The walls of the maze were 17 cm high and made of clear Perspex. The maze was supported on two stands that were 93 cm high. Testing was carried out in a large room that contained various large, distinctive objects. Illumination was provided by two fluorescent lights suspended approximately 95 cm above the maze.

**Procedure.** Animals underwent at least 7 days of pretraining, during which they learned to run down the stem of the maze to find food pellets at the choice point and in both food wells. During acquisition of the task, each rat underwent six massed trials daily. At the start of each trial, which consisted of two stages, three 45-mg food pellets (Campden Instruments) were placed in both food wells, and a wooden block was placed in one arm next to the choice point. The rat was then placed in the start box, and the guillotine door was raised. On this information trial, the animal was forced by the wooden block to enter the open arm and allowed to eat the food there. No retracing was permitted. The animal was then picked up and placed back in the start box, and the wooden block was removed. The guillotine door was then raised, and the rat was free to enter either arm. On this test trial, the rat was deemed to have chosen when it placed a back foot on either choice arm, whereupon the wooden block was placed behind the rat to stop retracing. If the rat alternated, in other words, entered the arm it had not visited on the information run, it was allowed to eat the food and was then returned to its cage. If the other arm was chosen, that is, the same arm as on the information trial, the rat was confined to the arm for approximately 10 s and then returned to its holding cage. In this manner, each animal was rewarded for selecting the arm it had not entered on the information trial. Each trial was separated by a 30-s intertrial interval during which the rat was placed in the home cage.

The sessions in the first 6 test days (36 trials) were considered practice sessions and were not counted when determining whether a rat had reached the criterion acquisition score of 16 correct responses in 3 consecutive days (18 trials). This feature was partly in response to the failure of some animals, both young and old, to complete 6 consecutive trials in a single session during the initial
training. This feature also ensured that the animals were fully familiar with the task before the next phase of the experiment began. This is an important aspect of the experiment because rats will spontaneously alternate and hence may reach the criterion score in spite of limited exposure to the reinforcing conditions.

In the second stage of the experiment, the retention intervals between the information trial and the test trial were varied. The rats underwent six sessions at each of three intratrial intervals, only one interval being used in any particular session. The sessions with intratrial intervals of 10 (the same as during acquisition), 30, or 60 s were given in a counterbalanced order. The animals were confined to their home cages during the retention interval for sessions with 30- or 60-s intratrial intervals.

Results

Analysis of the acquisition scores used nonparametric statistics in response to the skew distribution of the data (Figure 3, left). An initial analysis showed that although there was a trend for the male rats to require fewer sessions to reach the criterion acquisition score (Mann-Whitney U = 46; n = 11, 11) this difference was not significant. Consequently, the scores of the male and female subjects were combined for subsequent analyses of the effects of age on acquisition of this spatial task.

There were clear indications that the young rats required fewer sessions to reach the criterion score (16 correct trials in 3 days). The mean number of sessions to reach this score, after the arbitrary start on Session 7, was 4.6 for the young rats and 8.2 for the aged rats (Mann-Whitney U = 29, n = 8, 14, p < .05). Although 3 of the aged rats were later found to have pituitary tumors, their scores did not appear to be affected, and removal of their data does not alter the previous comparison (U = 22; n = 8, 11; p < .05). The difference between the young and the aged rats would have been considerably greater if not for 1 young female rat that, unlike any other animal, was unwilling to enter one of the T maze arms, even on information trials. This behavior lasted 10 sessions (Figure 3, left).

Figure 3 (right) shows the performances of the young and aged groups over the three retention intervals. Performance was compared with a three-way analysis, with age, sex, and delay as variables. Although there was a highly significant effect of increased delays on performance, F(2, 36) = 44.32, p < .001, there was no evidence that age, F(1, 18) = 2.50, or sex, F(1, 18) = 1.89, affected overall performance, nor was there any evidence of an interaction between the three variables (F < 1).

Discussion

As in the previous experiment, there was evidence that although aged rats may be impaired in the acquisition of a working memory task, they can perform normally over different retention intervals once the task has been mastered.

The acquisition deficit is in accord with other studies of spatial working memory in aged rats, most of which have used the radial arm maze (Barnes, Nadel, & Honig, 1980; Beatty et al., 1985; Ingram, London, & Goodrick, 1981; Wallace, Krauter, & Campbell, 1980). The findings from two other studies using a forced-choice alternation procedure in a T maze are, however, less clear cut. One study found no acquisition deficit in aged rats (Willig et al., 1987), whereas the other reported performance deficits (Lowy et al., 1985).

Although few studies have looked at the forgetting curves for the retention of spatial information, the results from this study are in accord with those of Willig et al. (1987), who found no differences in a comparable T maze task in which intratrial retention delays of up to 180 s were used. Considering these results, it may be noted that the two studies on the retention of the first four choices in a radial arm maze showed no evidence of an increase in forgetting rate with age (Beatty et al., 1985; Wallace et al., 1980).
It may be argued that the lack of a deficit with aging during the retention conditions in these studies was due to the shortness of the retention periods and that a deficit may have emerged with longer delays. Although we have no firm evidence on this point, the retention intervals used in these experiments were sufficient to produce highly significant changes in accuracy with delay but did not induce floor effects. Inspection of individual scores from Experiments 1 and 2 suggests that floor effects would have been observed in some of the young control animals had slightly longer delays been used. Also, the studies on retention of spatial information during radial arm maze performance reported normal rates of forgetting after delays as long as 15 min (Goodrick, 1968, 1972). We thereupon looked at the effect of having to remember more than one item or place at one time. This design followed the evidence that old rats perform more poorly as the number of choice points in a maze increases (Goodrick, 1968, 1972). We therefore tested both young and old rats on a T-maze in which the rat had to remember which two of four arms it had visited on the information trial.

Experiment 3: Spatial Delayed Nonmatching to Sample (I Maze)

As in the previous experiment, the rats were trained on a forced spatial alternation task in a T maze (spatial nonmatching to sample). The rats were then transferred to an I maze (Figure 4), in which they were forced into two arms on the information trial before receiving a double test trial. Therefore, the rats had to remember two arms concurrently.

Method

Subjects. The subjects were 16 rats (DA strain) that were housed and maintained as in the previous experiments. Eight of these rats (4 male and 4 female) were 3-4 months old at the outset of the experiment; of the remaining rats, 4 males were 14-19 months old (mean 17.3) and 4 females were 14-21 months old (mean 16.5). The experiment lasted 2-3 months. The mean weights of the rats at the completion of the study were as follows: old males, 305 g; young males, 266 g; old females, 203 g; young females, 192 g.

Apparatus. The first phase of the experiment was conducted in the same T maze as used in Experiment 2. For the second phase, an additional crossarm was fitted onto the stem of the T maze, thereby forming an I-maze (Figure 4). Both crossarms were 136 cm long and contained food wells 4 cm from the ends, making a total of four wells. The central stem of the maze was 97 cm long, and two wooden blocks were placed 20 cm apart in the middle of this central stem to form a start box.

Procedure. The first phase of the task was identical to Experiment 2, each animal being trained to a criterion of 16 correct responses over 3 consecutive sessions. As in the previous experiment, the scores from the first 6 sessions (36 trials) were ignored. Once the animals had reached this initial criterion, they received further training in the T maze until they had achieved a stricter criterion of 17 correct trials out of 18 over 3 consecutive sessions or had undergone a total of 20 test sessions (starting from Session 7). This additional training ensured that the alternation task was fully mastered before transfer to the more difficult I maze.

Each rat then underwent four double trials, that is, eight per session in the I maze. The rat was placed in the central start box, and each of the four food wells were baited with three 45-mg reward pellets (Campden Instruments). On the information trial the rat ran to the top choice point, where it was forced by a wooden barrier to enter either the right (R) or left (L) arm (Figure 4). After the rat had eaten the reward pellets, it was picked up and returned to the start box. The rat was allowed to run to the bottom choice point, where it was forced into one of the arms. Because there were four arms, there were four combinations of information trial; RR, RL, LR, and LL. The rat was then returned to the start box and allowed to run to the top choice point. The rat was rewarded if it selected the arm it had not entered on the information trial (i.e., alternated). The animal was then picked up and returned to the start box. If, however, the rat chose the wrong arm, it was briefly confined in that arm before being returned to the start box. This procedure was repeated immediately afterward in the bottom half of the maze. The rats were tested in groups of 4 and received spaced trials so that each pair of trials was separated by 6-8 min, the rats being returned to their home cages during the intertrial interval. These spaced trials were continued until the rats reached a criterion of 21 of 24 trials over 3 consecutive sessions, whereupon the animals underwent 10 sessions under massed trial conditions in which the intertrial interval of approximately 40 s was spent in the home cage.

Results

Figure 5 (left) shows the total number of sessions, starting from Session 7, required to reach the criterion score on the T maze (17 of 18 correct, maximum of 20 sessions), followed by the criterion score on the I maze (21 correct trials over 3 consecutive sessions). All but 1 rat (an old female) reached...
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As in Experiment 2, there were indications of a sex difference, the male rats learning the spatial task faster than the corresponding female rats. Indeed, we found that the male rats required significantly fewer total sessions overall to reach the acquisition criterion scores for both mazes combined ($U = 11.5, p < .05$, two-tailed test), regardless of age (Figure 5, left).

Although the young rats required fewer sessions overall to reach the same learning criterion, this difference was not significant (Mann-Whitney $U = 21.5, n = 8, 8$). With the exception of 1 old female rat, all animals transferred rapidly to the I maze and reached the criterion score within six sessions (Figure 5, left). Furthermore, a two-way comparison between the mean number of correct responses on the first 3 days in the I maze, after transfer from the T maze, showed that there were no differences between the performances of the young and old rats (young, $M = 89.6\%$; old, $M = 84.6\%$; $F(1, 12) = 1.67$), nor was there any evidence of a sex difference ($F < 1$).

In contrast, a significant age effect emerged during performance of the 10 sessions with massed trials (80 trials), which followed immediately after the animals reached the I maze criterion score (Figure 5, right), which all but 1 old rat managed. On these massed trials, the young rats averaged 91.6% correct responses, whereas the aged rats averaged 81.4%, and an ANOVA confirmed a significant age effect, $F(1, 11) = 7.24, p < .025$. There was, however, no effect of sex, $F(1, 11) = 1.45$, nor was there evidence of an interaction between sex and aging ($F < 1$).

Discussion

Unlike in the previous experiment, the aged rats showed no clear impairment in the acquisition of a test of spatial working memory. Furthermore, the aged rats showed no difficulty in transferring to the I maze, where they performed at the same level as the young rats when the trials were spaced. However, a clear deficit did emerge when the trials were massed.

Although running speeds were never formally measured, it is difficult to ascribe this deficit merely to a slowing of the aged rats and hence to a selective increase in the retention times. If such a change had occurred, one would have expected its effects to be apparent in the initial performance on the I maze when the trials were spaced or on the performance trials with the T maze (Figure 3, right). One explanation of these results is that a persistent deficit with aging only emerges as the information load is increased or where there is considerable proactive interference. Thus, after acquisition, aged rats are not impaired with massed trials on a T maze (Experiment 2) but are impaired on an I maze. This result can also be interpreted as being consistent with the absence of an acquisition impairment found in a comparable T maze forced-alternation task (Willig et al., 1987), in which the intertrial interval was longer (75–90 s), thereby reducing potential interference effects. There is additional supporting evidence from other studies for both of these proposals (Barnes, 1979; Barnes et al., 1980; Goodrick, 1972), although in many instances information load and proactive interference clearly are tightly bound so that when one increases, so does the other. The difficulty of independently assigning in-

![Figure 5. Spatial nonmatching-to-sample results (I maze). (Left: Combined acquisition sessions required by individual animals to reach the criterion scores on the T maze and I maze. Animals that required the maximum of 20 sessions on the T maze are indicated by asterisks. Right: Total correct trials for each animal from 10 consecutive sessions [maximum = 80] with massed trials.)](image-url)
formation load, however, clearly limits the use of such an explanation. For example, in this experiment, information load cannot simply be equated with task difficulty, as measured by performance levels, because the mean percentage scores in the massed condition in Experiment 3 were higher than those found during the delay conditions in Experiments 1 and 2, when no age effect was apparent.

An alternative explanation centers on the spatial nature of the task and the clear evidence that aging may, under some circumstances, affect the retention of spatial information (Barnes & McNaughton, 1985; Rapp, Rosenberg, & Gallagher, 1987). With the I-maze and massed trials, a greater demand may have been placed on the animals' abilities to remember which of the four locations had been visited, an interpretation consistent with deficits that have been repeatedly observed with the radial arm maze (Barnes et al., 1980; Beatty et al., 1985; Ingram et al., 1981; Wallace et al., 1980; Willig et al., 1987). Furthermore, there is evidence that aged rats are more reliant on response cues than on spatial cues in solving spatial problems (Barnes et al., 1980), a difference that could of course be a consequence and not a cause of poor spatial memory. Nevertheless, such a bias might contribute to this result, because the use of an I maze and massed trials might be thought to penalize rats that remembered which body turns they had made rather than which location they had visited, because there are only two turns but four locations to be distinguished.

Evidence of a sex difference emerged during the acquisition of the T maze alternation task, the males performing better than the female rats. This difference remained when the single T-maze acquisition performances from Experiments 2 and 3, which used identical conditions, were combined (U = 100, n = 19, 19, two-tailed test, p < .02). This sex difference is consistent with findings from other studies that have shown that male rats typically perform better on spatial tasks, including those taxing working memory (Beatty, 1979; Eion, 1980; Tees, Midgely, & Nesbit, 1981). It may be noted that the only indication of a sex difference in the nonspatial test of working memory (Experiment 1) was in the opposite direction; in other words, there was superior retention by the female rats after the longest delay. Although a sex difference in the spatial tasks may have added variance to the data and obscured differences in the acquisition of the tasks in Experiments 2 and 3, it cannot account for the absence of an age effect on retention in Experiment 2 or for the difference that emerged in the massed-trials condition in Experiment 3.

General Discussion

In this study, we compared young and aged rats on the acquisition and subsequent performance of a spatial and a nonspatial test of working memory. In Experiments 1 and 2, we found that whereas aging could impair the rate of acquisition of such tasks, it did not alter the subsequent forgetting curves for single items or single locations over delays of up to 60 s. These two experiments clearly underline the value of equating performance levels before rates of forgetting can meaningfully be compared and highlight the difficulty of assuming that an apparent learning difficulty reflects a deficit in the remembrance of the test stimuli. In addition, some other recent studies of working memory using the radial arm maze (Beatty et al., 1985; Wallace et al., 1980) and a T maze (Willig et al., 1987) have also reported normal forgetting rates in aged rats. Also, once learning is equated, the modal finding from human studies is that aging does not affect retention (Craik, 1977; Eysenck, 1977).

Our findings of normal forgetting rates on tests of working memory may be contrasted with reports that aging impairs the retention of passive avoidance tasks (Bartus et al., 1980; Kubanis & Zornetzer, 1981; Martinez & Rigter, 1983). Because these two classes of memory tasks differ considerably, direct comparisons cannot be made. Nevertheless, all of these passive avoidance tasks involve one-trial learning, which often rules out the possibility of matching acquisition levels before retention is tested. Given the evidence from previous studies (Beatty et al., 1985; Doty, 1968) that factors such as neophobia and emotionality may influence acquisition, retention deficits must be interpreted with care.

There is convincing evidence that aged rats show a selective impairment in the ability to use spatial information. For example, aged rats are impaired on the Morris water maze, and this impairment cannot be related to differences in swimming ability or motivation (Rapp et al., 1987). Similarly, aged rats are poor at learning an escape location and furthermore display faster forgetting of that location than do young rats (Barnes & McNaughton, 1985). These findings are in contrast to the reports of good memory retention of arms entered in the radial arm maze, once the task has been mastered (Beatty et al., 1985; Wallace et al., 1980), or the performance of the animals in Experiment 2. A resolution of these apparent inconsistencies may lie in the strategies used by the animals to solve the tasks. Specifically, spatial tasks that aged rats can solve and remember involve the use of response strategies. Thus, with prolonged training with a T maze or a radial arm maze, aged rats may learn to use and remember their responses to solve the task at normal or near-normal levels. This finding is consistent with evidence that old rats are more reliant than young rats on response cues (Barnes et al., 1980). This finding in turn suggests that clear distinctions between spatial and nonspatial memory capabilities may be necessary in aged rats and that within the class of spatial memory, further distinctions may prove important.

References