

A Species Difference in Visuospatial Memory: A Failure of Memory for What, Where, or What is Where?

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Four experiments were conducted to determine why rhesus monkeys (*Macaca mulatta*) perform so poorly on a visuospatial memory test modeled after a popular children's game (Concentration). In these studies, four different memory tasks were administered to ascertain whether monkeys show limitations in visual memory (memory for which images had been seen), limitations in spatial memory (limitations of what locations had been visited), or limitations in the coordination of these two modalities (memory for what images are located where). The data indicate that the monkeys could remember visual information when there were no spatial demands. The monkeys could also remember spatial information when there were no visual-memory demands, although performance on this spatial-memory task was not as accurate as had been predicted. However, when visual and spatial memories had to be coordinated—memory for what was where—performance was no better than chance. Hypotheses were discussed for why the monkeys, but not human participants, struggle to coordinate visual and spatial memory. Perhaps this represents an area where humans use verbal working memory—a mnemonic strategy that is presumably unavailable to nonhuman primates—to facilitate the maintenance and cross-referencing of visual and spatial information.

The research paradigms used in studies of human short-term memory or working memory (not synonymous terms, but the distinction is not important to the present investigation) vary as a function of the modality of the stimuli. The vast majority of studies in the literature pertain to memory for verbal material, and a variety of recall paradigms are available for these tests (see, e. g., those summarized by Baddeley, 1986, 1990, 1992). For visuospatial stimuli (those not easily recoded verbally), pure recall procedures are more difficult to implement. For this reason, investigations of visuospatial memory are typically based on recognition or completion tasks (see Phillips & Christie, 1977). In this respect, studies of human memory for visuospatial stimuli are comparable to studies of memory by nonhuman animals, in that comparative studies of short-term memory almost always employ a recognition paradigm of some form. These procedures include variations of the delayed matching-to-sample task (e.g., Phelps & Roberts, 1994), the delayed nonmatching to sample task (e.g., Tavares, 2002; Mishkin & Delacour, 1975), the delayed response task (e.g., Kojima, 1980; Pontecorvo, 1996), and the delayed same/different paradigm (e.g., Washburn & Astur, 1998), including the serial-probe recognition task (e.g., Sands & Wright, 1982; Smith, Shields, Allendoerfer & Washburn, 1998).

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One can add a recall component to recognition tasks in several ways, for instance by providing a list of images and requiring ordered recognition (i.e., recognize items but recall order). Another memory task that adds a recall component to recognition procedures is the Concentration task. In this task, participants must turn over a card and recognize whether the image on the card has been seen before. Additionally, the participant must recall the location of the card that matches that particular image is located. Another useful feature of the Concentration task is that one can easily manipulate the difficulty of the task by changing the number of pairs of images that must be located. For these reasons, variations of the Concentration task have been used to test the visuospatial memory abilities of preschool children, teenagers, adults, and aged adults (Arnold & Mills, 2001; Baker-Ward & Ornstein, 1988; Schumann-Hengsteler, 1996a, 1996b).

The concentration paradigm has also been used to compare the visuospatial memory performance of humans and nonhuman primates (Washburn & Gulledge, 2002). The results from this study were surprising, however. Whereas human children, adults, and the aged have generally performed the task well, albeit with interesting if inconsistent age differences, the rhesus monkeys tested by Washburn and Gulledge performed at or worse than chance levels across all conditions, including on the easiest 2-pair problems. That is, the monkeys were able to find matching pairs of stimuli, and completed many thousands of concentration-task problems. Additionally, the data indicated that the monkeys were not responding randomly, but were in fact trying to locate matching stimuli hidden in the arrays of computer-generated "cards." Thus, it seems likely that the monkeys knew that the goal of the task was to find matching images. Notwithstanding, the monkeys would occasionally perseverate on particular errors, repeating the same mistake or subset of mistakes dozens of times. Consequently, their performance on average was significantly worse than chance on difficult problems, and no better than chance on any level of problem. This pattern of results was consistent across animals, across stimulus types, across numbers of pairs of stimuli, and was not changed by training designed specifically to eliminate perseverations.

Why would this be the case? If one accepts the interpretation (Washburn & Gulledge, 2002) that the rhesus monkeys were trying to find matching images, why did they repeat particular errors that themselves had no obvious rhyme or reason? It seems feasible that the monkeys' memory problems reflected an overload of the visual or spatial memory system, such that errors were particularly likely when either the "memory for what" demands or the "memory for where" demands (or both) became too great. In the simplest form of this argument, the monkeys would perform well at some levels of difficulty (e.g., with two or three pairs of stimuli) but perform poorly whenever the difficulty of the task exceeded the limits of memory (e.g., for four or more pairs of stimuli). However, this simple case was certainly not the case: The monkeys often perseverated even on the easiest version of the task (e.g., with just two pairs of images). Conversely, the monkeys often performed very well even on the most difficult versions of the task (e.g., problems with six pairs, although perseverations were indeed more likely and more robust with these problems). Notwithstanding, we reasoned that it should be possible to identify, through a series of task manipulations, whether the concentration-task performance reported for monkeys in the previous study was a reflection

primarily of visual (what) or spatial (where) limitations.

For example, it is possible that the animals were confusing the stimuli from problem-to-problem, and thus that differential levels of proactive interference (or, alternately, an increased sensitivity by the monkeys to proactive interference) accounted for the species differences in performance. There is substantial literature on the build-up and release of proactive interference (or inhibition) and its effect on memory. It is apparent that this across-trial effect is responsible for some portion of forgetting in typical memory studies in which participants must complete a series of trials, particularly when the to-be-remembered stimuli are repeated (or are similar, as in from a single category) across consecutive trials. Perhaps rhesus monkeys are particularly susceptible to this kind of trial-to-trial interference, and thus that this susceptibility led to the species differences reported in concentration-task performance. To address this possibility, we reduced the demands on episodic memory by testing the monkeys on a task in which the stimuli did not repeat from problem to problem.

Experiment 1

Method

Subjects. Six adult male rhesus monkeys (*Macaca mulatta*) were tested in this study. Prior to this experiment, the monkeys (age range 6 to 16 years) had been trained to manipulate a joystick to respond to computer stimuli on numerous tasks, including the Concentration task used in this experiment (Washburn & Gulledge, 2002). The animals were tested in their home cages with ad libitum access to the computerized test system. Thus, they worked or rested whenever they chose, and were not reduced in body weight for purposes of testing. Water was continuously available, as were toys and other manipulanda for enrichment.

Apparatus. A computerized test system was available to each monkey. The system consisted of a DOS-based personal computer, a 13-inch color monitor, an analog joystick oriented vertically (i.e., so that the joystick handle extended directly toward the monkey, making cursor movements isomorphic to joystick movements), a pellet dispenser, and an external speaker-amplifier (see Rumbaugh et al., 1989, for details). Correct responses were rewarded with 97-mg fruit-flavored chow pellets (P. J. Noyes; Lancaster, NH, U.S.A.) delivered automatically using Keithley interfaces (PIO12 and ERA01).

Task. The computerized version of the concentration game was identical to that described by Washburn and Gulledge (2002, Experiment 2). To begin each trial, a grid of 14 squares or cells appeared around the perimeter of the computer screen (see Figure 1). Some of these cells were selected randomly and marked with a large blue plus-sign (+), indicating that these cells were active "cards" for that trial. A small white plus-sign was positioned in the middle of the screen (and thus surrounded by these 14 cells). Bringing the cursor into contact with one of the computer-generated cards caused the card to "flip over," or reveal the image concealed at that location. The image remained visible as the cursor returned automatically to the midscreen location, allowing the subject to select a second card. If the images revealed in these two locations were identical (i.e., they matched), then a tone sounded and pellets were dispensed. If the images did not match (an error), a 50-Hz buzz was produced for 1 s and the images were replaced by the original blue plus-signs (i.e., as if the card turned back over to conceal the images). Thus, each problem consisted of a series of trials in which the subjects attempted to locate all of the matching pairs of stimuli hidden in the array of computer-graphic cards. For the present experiment, each problem consisted of four pairs of stimuli (eight cards total), a moderate level of task difficulty, but one at which performance was consistently worse than chance in the Washburn and Gulledge (2002) data.

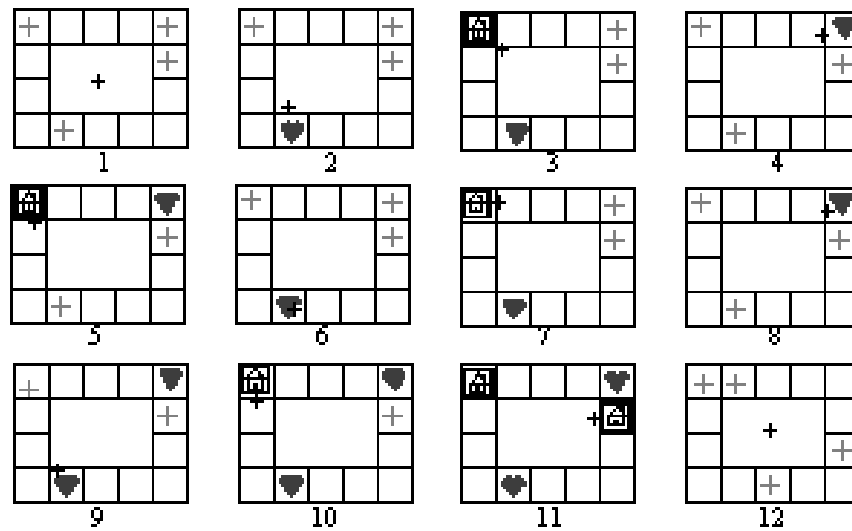


Figure 1. Sequence of responses on a 2-pair concentration problem, showing perseverative errors and the beginning of a new 2-pair problem (frame 12).

To test the possibility that performance on the task reported in the previous study (Washburn & Gullledge, 2002) reflected the build-up of proactive inhibition, only problem-unique stimuli were employed in the present study. That is, each problem used four pairs of line-drawn or clip-art images, and then these images were discarded in favor of new images for each new problem. These images were comparable to the ones used in the previous research, but had never before been used in tests with the monkeys. Thus, the monkeys' memory of where the pictures any particular image were located was irrelevant on subsequent problems, as the pictures were not used again.

Procedure. A new pool of 200 stimuli was drawn for this study. Each monkey was tested on 50 four-pair problems, in which each problem used a different set of four stimuli. The order in which the stimuli were used was randomized across monkeys. Following the last of these unique-stimulus problems, the Concentration task was administered to each monkey for an additional 1,000 problems using the same library of eight stimuli (i.e., those stimuli from the last two problems of the stimulus-unique condition). On each of these 1,000 problems, the number of pairs to find was selected randomly (between 2 to 6 pairs), as was the specific images that were selected for these pairs and the locations of the pairs within the array. These latter problems were administered to provide a baseline that could be compared to the Washburn and Gullledge (2002) data and against which the effect of nonrepeating stimuli could be determined.

Results

The key comparison in this study was how the monkeys performed on four-pair problems with problem-unique stimuli versus on four-pair problems in which the same stimuli were used in each problem. (For the sake of parity, only the first 50 repeated-stimulus problems for each monkey was used for this comparison to the 50 unique-stimulus problems.) The monkeys produced significantly fewer errors when the stimuli were novel on each problem (18.20 errors, $SD = 3.05$) than when the same library of stimuli were used on each problem (19.20 errors, $SD = 2.75$), $t(5) = 2.61$, $p < 0.05$.

However, as can be seen in Table 1, performance was still remarkably poor across conditions—including with the problem-unique stimuli. To calculate the number of errors that would be expected by chance alone, Monte Carlo computer simulations of 50-problem blocks of four-pair problems were conducted. In one

million simulated 50-problem blocks, an average of even 15 or more errors per four-pair problem was observed with a probability of only $p = 0.006$. Thus, performance was significantly improved when problem-unique stimuli were used, but remained significantly worse than chance on four-pair problems ($p < 0.01$) even with these nonrepeating stimuli. Indeed, Table 1 reveals performance to be generally poor relative to chance across difficulty levels.

Table 1
Mean Number of Errors as a Function of Condition (Problem-Unique vs. Repeated Stimuli) and Number of Pairs.

	2 pairs	3 pairs	4 pairs	5 pairs	6 pairs
Problem-unique stimuli			18.2 errors (3.05)		
Repeated use of same stimuli	2.2 errors (0.22)	7.7 errors (1.11)	19.8 errors (2.76)	29.8 errors (7.14)	40.0 errors (9.70)
Chance	2 errors	6 errors	12 errors	20 errors	30 errors

Note. Numbers in parentheses are standard deviations. Chance levels were determined by computer simulation.

Discussion

These results suggest three conclusions. First, the monkeys were performing in this study comparably to how they performed in the earlier (Washburn & Gullledge, 2002) experiments. Second, this level of performance was improved slightly but reliably when stimuli did not repeat from problem to problem. Finally, the proactive interference that comes from repeating stimuli from problem to problem is not the cause of the monkeys' characteristically poor concentration-task performance relative to chance, because even with problem-unique stimuli this performance level was significantly worse than chance. As with the previous experiments, the monkeys completed many problems efficiently; however, occasionally the animals would repeat a particular error or subset of errors for many consecutive responses. These perseverations were observed at all difficulty levels (from two pairs to six pairs), were seen in the problem-unique as well as the repeated-stimulus conditions, and drove the average number of errors up over chance across the board.

Experiment 2

If the monkeys' perseverations on the Concentration task were not the result of inter-problem interference of the type studied in Experiment 1, what might be the source? Because perseverations appeared even at the lowest level of task difficulty (two pairs), we next considered the possibility that the capacity of monkey memory is particularly small—or more specifically, that their capacity for visual memory (“what” memory) is particularly small. If indeed this hypothesis is true then errors, including perseverative errors, would occur when the number of to-be-remembered items exceeds the capacity of visual memory. From the existing data (Washburn & Gullledge, 2002, as well as the data from Experiment 1 of the

present study), we might anticipate this capacity to be fewer than four items (i.e., two pairs of items, assuming that identical copies of an image are stored as separate to-be-remembered items). On the one hand, one might make the case that the capacity of the visual working memory is as small as one item. Phillips and Christie (1977) used a matrix-completion task to study the capacity of visuospatial memory for humans and estimated that capacity to be one item. In support of their claim, they reported that the recency effect for lists of to-be-recognized visual stimuli is typically limited to a single item. Sands and Wright (1982) and others using a serial-probe recognition task to study the capacity for remembering visual information over short periods of time have also found a terminal-item recency effect, but tend also to report better-than-chance (but less-than-the-most-recent-item) performance for all items in lists of four or more to-be-remembered images. This would indicate, on the other hand, that short-term memory has a capacity of several items (enough to perform well on the easiest conditions of concentration) both for monkeys and for humans. We designed a new task to explore this question.

Method

Subjects. Two of the animals from Experiment 1 were tested in this study. These macaques (6 years old at time of testing) were selected arbitrarily. Each had extensive experience with joystick-based computerized tasks, including on various forms of delayed matching-to-sample tests of memory. Neither had been exposed to the specific task used in this study, however.

Apparatus and Task. The apparatus was identical to that described for Experiment 1. A new task was designed, however, to permit assessment of “memory for what” without demands from “memory for where.” Each trial began one to four sample (to-be-remembered) stimuli presented in randomly selected positions around the perimeter of the screen. (The positions were selected from the cell locations used in the Concentration task; however, the grid normally used to define these cells in concentration was not used in the present task.) The stimuli were the line drawings used in the previous study. A cursor (a small plus-sign) was also presented randomly on the screen. In the middle of the screen, a small white circle (2.5 cm diameter) was presented. The monkeys had been trained on many previous tasks to manipulate the joystick so as to bring the cursor into such a circle to start the trial.

When the cursor was positioned within the circle, everything on the screen except the cursor disappeared. In this way, a monkey could initiate a trial whenever he was ready to have the stimuli disappear. After a 5 s delay, stimuli were presented again in the positions occupied at trial outset. However, all but one of the stimuli presented in this recognition phase was new (i.e., different from the original images). Thus, if there were originally two sample stimuli presented on the screen, one of these images would appear in its original location during the recognition phase and a new stimulus would appear where the other stimulus was located (see Figure 2 for a schematic of this trial sequence). The monkeys’ task was to move the cursor to the old stimulus, that is, to recognize which stimulus had appeared as one of the sample images. In this way, we were able to test the monkeys’ memory for varying numbers of images under conditions in which stimulus position was irrelevant.

Procedure. Each of the monkeys completed 100 trials in which the number of sample stimuli was titrated between two and four, contingent on performance. That is, the monkey began with a two-sample problem; if they correctly identified the sample during the recognition phase, the next trial would be a three-sample problem. Recognition errors caused the next trial to become easier, but never easier than a two-sample problem. Following these training trials, each monkey 10 blocks of 60 trials in which the number of sample stimuli was randomly selected (2, 3, or 4) on every trial. The library of eight stimuli (the same images that had been used in Experiment 1) used in these trials was changed on each block.

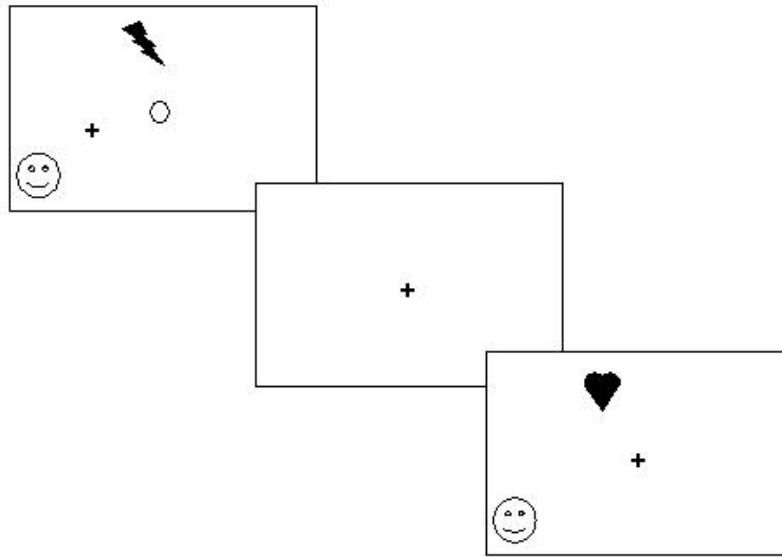


Figure 2. Schematic of sequence of screens that make up a two-stimulus trial for the task in Experiment 2. A trial began with a screen like the one on the left.

Results

The monkeys learned the new task quickly, as evidenced by the fact that performance (i.e., moving to the single “old” stimulus in the recognition phase) was significantly above chance within the first block of 100 trials. Because no trend was evident across the 10 blocks of trials (all autocorrelations were nonsignificant, $p > 0.10$), the test data were grouped by animal and analyzed across blocks as a function of memory load (number of sample stimuli). A significant effect of memory load was observed, $F(1, 17) = 44.87$, $p < 0.01$, but accuracy was significantly better than chance in all conditions. Contrast analyses revealed that performance declined significantly between the two-sample condition ($M = 89\%$) and the three-sample condition ($M = 75\%$), and also between these conditions and the four-sample trials ($M = 60\%$; all $p < 0.01$).

Discussion

Although performance was far from perfect in any condition, the monkeys performed reliably better than chance even in the most difficult condition used in this study (chance = 25% for the four-sample problems). This indicates that the monkeys are capable of remembering which stimuli had been recently seen with memory loads of at least four items. These data are consistent with previous findings from serial-probe recognition procedures, and indicate that the capacity of visual memory should be sufficient to support good performance on the Concentration task.

Two caveats must be acknowledged about these data and the task from which they were generated. First, the present task requires recognition memory of which stimulus was a sample on each trial. This is an easier task than one that might require recall of any single stimulus from the to-be-remembered samples.

One could make the case that the Concentration task has more of a recall component than the present, multiple-alternative delayed matching-to-sample task. However, it is difficult to untangle “recall whether you saw this stimulus” from “recall where you saw this stimulus” in the Concentration task itself. The present task, at a minimum, provides an assessment of the monkeys’ ability to remember whether they had seen a group of stimuli under conditions in which the animals could not know in advance which stimulus from the group would be probed and in which there was no spatial-memory requirement. This contention that the monkeys can remember what stimuli they have seen, at least up to a memory set of four items is also consistent with the finding from Washburn and Gullledge (2002) that the monkeys do not revisit old “cards” in the Concentration task until they have located at least one match (i.e., they remember what images they have seen).

Second, one might suggest that a memory load of four items on the present task is equivalent to the memory load in only the easiest version of the Concentration task (i.e., the two-pair condition, if one assumes that each copy of the matching images is remembered as a separate item in memory). That is, one might suppose that the Concentration task is much more difficult than the present delayed matching task, and thus that the better-than-chance performance in the most difficult condition of the task from Experiment 2 tells us little about why performance was so poor in the task of Experiment 1. However, even on those relatively simple two-pair concentration problems, perseverative errors were observed—admittedly infrequently, but more often than would be suggested by the significantly better-than-chance accuracy in “memory for what” as suggested here.

If indeed one accepts the assertion that the monkeys have good “memory for what” when spatial demands are kept minimal, might their concentration-task problems stem from limitations in “memory for where”? That is, how would they perform on a task with various spatial-memory loads but on which visual memory (memory for what) is irrelevant?

Experiment 3

Such a task exists and is widely used for memory studies. Variations of the radial-arm maze paradigm have been used as a test of spatial memory with numerous animal species, but primarily rodents (e.g., Lipp et al., 2000; Olton, 1977; Tolman, 1946). Radial-arm maze testing involves the baiting of some number of alleys and observing the efficiency with which animals search the arms for food. Visiting an alley allows the animal to find the food there, but revisiting an alley is not rewarded. Rats are able to remember at least 32 different alleys (Roberts, 1984), as evidenced by the low probability of revisiting alleys that had been previously entered, even when nonspatial memory cues are controlled.

In this experiment, rhesus monkeys were tested on a computerized task modeled after the radial-arm maze rather than the Concentration task, and thus that required spatial memory with no visual-memory demands. Note that this task was quite different from the memory tasks of Experiments 1 and 2, both of which required memory of “what had been seen.” The present task was designed to isolate the memory of “where had been visited” component of the Concentration task. We hypothesized that the macaques would have little difficulty in keeping track of which spatial locations had been visited. Conversely, if limitations in

spatial memory were at the root of the monkeys' problems on the Concentration task—if they perseverated on concentration errors because they could not keep track of which cards they had recently visited—then problems with the present task should have been observed.

Method

Subjects and Apparatus. The six monkeys from Experiment 1 were tested in this experiment. These monkeys were tested with the same computerized test systems that were used in the previous studies. Undergraduate volunteers ($N = 32$, M age = 20.04 years, 23 females) were also tested. These students volunteered in exchange for course credit.

Task. A grid like that used in the Concentration task was presented on the screen. However, the colors were reversed from the Concentration task (a black grid on a white background for the present version). From 2 to 12 randomly selected cells were marked as “active” each with a small (1.25 cm diameter) blue dot. Moving the cursor into an inactive cell had no effect, but moving the cursor into contact with one of the dots was recognized as a response. When a dot was touched for the first time in a problem, a beep was produced and a pellet was delivered. The dot remained visible on the screen, and it was impossible to discriminate visually (i.e., without spatial memory) which sites had been visited and which were untouched on that problem. Each subsequent visit to that dot (or any other touched already in that problem) resulted in buzzing noise for 2 s. After each response, reinforced or not, the cursor returned to the center of the screen. This continued until each of the dots had been touched at least once, whereupon a 15-s intertrial interval intervened before a new problem was presented with 2 to 12 randomly selected cells again marked by dots as active. Thus, efficient responding would require the subject to touch each dot once and only once per problem, “collecting” each of the available pellets without wasting any moves to previously visited sites. Inefficient responding would involve repeated contact with the same dot or group of dots within a problem, perseverating on errors before finally collecting the last of the available pellets.

Procedure. Each monkey was initially trained on 50 problems with 2 dots and 50 problems with 4 dots. Subsequently, each monkey completed at least 12,000 problems of the task. On each problem, either 2, 4, 6, 8, 10, or 12 dots—corresponding to the number of pellets that was available for that problem—was positioned randomly within the grid on the screen. Each human participant was tested on the same task for 120 problems. They received instructions prior to testing (including instructions not to use a finger or other nonmemory cue to keep track of which dots had been touched), but received no rewards other than the auditory feedback during the session.

Results

The monkeys moved the cursor into contact with the dots from the very first trial and quickly learning not to revisit dots that had previously been touched. The monkeys also moved without hesitation to the dots within the new array (even in old positions) each time a fresh problem followed the inter-trial interval. Examining the monkeys' performance across difficulty levels by blocks of 1,000 problems, performance improved slightly across the first three blocks (from an average of 8.5 errors, to 7.6 errors, to 7.4 errors), but remained stable for the remainder of testing. That is, it seems reasonable to conclude that the data analyzed here reflect mature, asymptotic performance.

The results of this study are depicted in Figure 3, which shows the mean number of errors (revisits to dots within a problem) as a function of the number of dots for humans, monkeys, and computer-simulations of chance. Computation of chance involved one million computer-simulated blocks of 2,000 problems at each level of task difficulty (2, 4, 6, 8, 10, and 12 dots), selecting active dots randomly with replacement. As can be seen in the figure, monkeys performed reliably and

dramatically worse on the task than did humans; however, the monkeys were significantly better than chance at all levels of task difficulty ($p < 0.05$; that is, errors as infrequent as those observed for the monkeys were obtained on fewer than 5% of the blocks of computer-simulated problems.

Consider these same data in a different way: By chance alone, 67% of the 2-dot responses would be correct, and the percentage would decline systematically until on 12-dot problems only 33% of the responses would be correct by chance alone. (These estimates of chance were again produced by the Monte Carlo computer simulation of blocks of problems.) For the monkeys, mean accuracy (i.e., number of rewarded responses per problem divided by the total number of dots touched per problem) ranged across difficulty levels from 85% for 2-dot problems to 39% for 12-dot problems. Mean accuracy for humans never dipped below 98% at any difficulty level in these data.

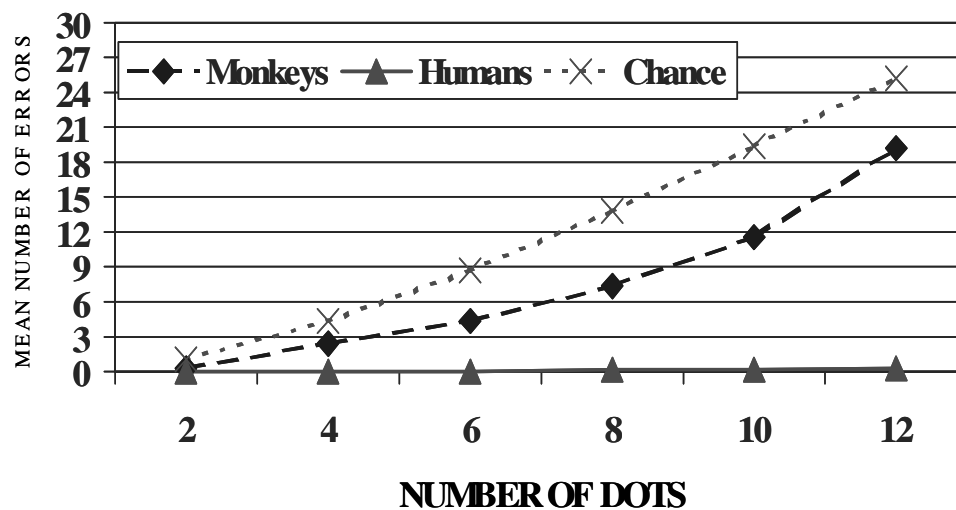


Figure 3. Mean number of errors as a function of species and number of dots for the task in Experiment 2.

Whatever this reveals about memory, it also reflects an interesting species difference in strategy. Humans were able to avoid errors by selecting dots consecutively (e.g., starting with the dot closest to the top-left position and moving clockwise until the trial ended). In this way, human participants greatly reduced the memory load for the task. Rather than remembering all of the sites that had been visited, humans in effect only had to remember which dot they had visited most recently and in which direction they were moving. Monkeys, in contrast, tended to select dots beginning with those closest to the cursor and ending with those most distant. This haphazard pattern of foraging for dots required extensive memory of what locations had been visited already (or which had yet to be visited on that problem).

Discussion

Whereas the results of Experiment 1 and 2 were clear, the present findings are controvertible. In Experiment 1, the monkeys proved unambiguously incapable of performing the Concentration task efficiently. In Experiment 2, the monkeys

were reliably good on a memory task requiring visual but not spatial memory. In the present study, the monkeys were indeed significantly better than chance on the task, but performed much more poorly than was predicted on the basis of human performance (or rodent performance in traditional radial-arm mazes). The macaques knew that the goal of the task was to touch the dots without repetitions (or, at least, this was the efficient way to perform), and did so using memory rather than random selection of dots. They did not use a simplifying strategy as did the humans (which was fortunate, because it would have minimized the usefulness of the present task for estimating the capacity of spatial memory), but neither did they perseverate on particular errors as was the case in previous Concentration-task tests (Experiment 1; Washburn & Gullledge, 2002). Rather, their errors followed no specific pattern, and appeared to be memory failures in the traditional sense. Indeed, there was a trend for errors to be related to the position of dots on the previous problem. On 4-dot problems, for example, errors were twice as likely to dots that occupied positions active on the previous problem than to dots that occupied new positions.

We conclude from these data that the monkeys do have the capacity for spatial memory. That is, they can remember where they have visited—although their memory is far from perfect. Although the difference in performance between monkeys and humans might suggest that a spatial memory deficit underlies the monkeys' poor concentration-task performance, we conclude that spatial memory failures account at best for only some of the concentration errors. The failures by the monkey to remember where they had and had not visited do not have the characteristic pattern of the perseverative errors that characterize memory for “what stimulus was located where.” Indeed, the monkeys' inability to remember where they had visited was nonetheless significantly better than chance in even the most demanding (12-dot) condition of the present task, whereas it was reliably worse than chance on the Concentration task in even the easiest condition.

Experiment 4

Experiment 4 was designed to contrast the monkeys' performance on two similar tasks: a purely spatial memory task and a visual+spatial (visuospatial) memory task. There were four possible outcomes of this experiment, and three of the possibilities would provide useful information about the limits in monkeys' memory. First, the monkeys might have failed to perform better than chance on either task. Such a finding would be interpreted as indicating that the monkeys cannot remember spatial positions (and thus would oppose the findings of Experiment 3). Alternatively, the monkeys might have performed above chance on the spatial task but at chance levels on the visuospatial task, indicating that they could remember “where” but not “what was where.” Third, the monkeys might have performed well on both tasks, suggesting that they can remember both “where” and “what was where.” Such a finding would indicate that the concentration failures observed in Experiment 1 are idiosyncratic to that task, possibly reflecting the role of strategy or other nonmemory mechanism. It did not seem reasonable to expect the fourth possible outcome, as the monkeys should not have performed well on the visuospatial memory task but poorly on the task with spatial demands alone.

Method

Subjects and Apparatus. Two of the rhesus monkeys from Experiment 3 tested on the two tasks of this study. The other monkeys were unavailable for testing in this study. The same apparatus was used, but two new tasks were written for this study.

Spatial Memory Task. Each trial began with a circle (0.5 cm) in the middle of the screen, surrounded by 2 to 5 boxes. Each box measured 4 cm by 5 cm and was equidistant (about 7 cm) from the middle of the circle. Adjacent boxes were also equidistant from one another. One of the boxes contained the target stimulus for that trial. Target stimuli were randomly selected drawings of the same type used in Experiments 1 and 2. A cursor (a plus sign) also appeared in random position along the bottom of the screen.

To begin the trial, the monkey manipulated the joystick so as to bring the cursor into the center of the circle. At this point, the cursor and the target stimulus disappeared for a brief retention interval, during which the empty stimulus boxes remained visible. After the retention interval, the target stimulus reappeared, but in the center of the screen, in the position previously occupied by the cursor. In fact, the target stimulus was now the cursor and moved around the screen in response to joystick manipulation. Consequently, the animals were required to move this target stimulus into the box where it had previously appeared. Note that the identity of the target stimulus was irrelevant to performance. The monkeys only had to remember *where* the image had appeared. Correct responses resulted in the delivery of one 97-mg fruit-flavored chow pellet, whereas incorrect responses resulted in a 10-s timeout filled with a buzzing noise.

Visuospatial Memory Task. The visuospatial task was identical to the spatial task with one exception: During the initial presentation of the target stimulus, each of the other boxes also contained a randomly selected (nontarget) image. That is, the monkey would see 2 to 4 stimuli located in boxes and arranged at equal intervals around a small circle. When the cursor (plus sign) was brought into the circle, the cursor and all of the stimuli (but not the boxes) disappeared. Following the retention interval, the target stimulus appeared midscreen as the cursor. Again, the monkey was required to move the target stimulus into the box where it had previously been presented. Unlike in the spatial-memory task, however, the present version required the monkeys to remember which stimuli appeared in each of the slots because there was no way to determine at trial outset which stimulus was the target image. That is, the task required memory of *what* was *where*.

Procedure. Each monkey completed 1,000 trials of the spatial-memory task with a 0-s retention interval, followed by 1,000 trials on the same task with a 1-s retention interval. Each monkey also completed at least 1,500 trials on the visuospatial-memory task with a 0-s retention interval.

Results

On the spatial-memory test, we used both 0-s and 1-s retention intervals to eliminate the chance that the monkeys were using afterimages and visual persistence to solve the task. Because performance was comparable in this task following the 0-s and 1-s retention intervals ($p > 0.10$), these conditions were collapsed for further analyses.

Performance on the two tasks was compared across difficulty levels (2, 3, or 4 boxes). Performance was significantly better on the visual-memory task than the visuospatial-memory task (60% versus 38%, respectively, excluding the 5-box trials that were unique to the visual-memory task), $z = 11.58$, $p < 0.01$. A significant main effect for task difficulty was observed, $F(2, 2) = 178.36$, $p < 0.05$, and this variable did interact reliably with task type, $F(2, 2) = 26.06$, $p < 0.05$. This main effect was predictable and not interesting, given that increasing the number of boxes reduces the likelihood of being correct by chance. The interaction,

depicted in Figure 4, is quite meaningful, however, with respect to the predictions described for this study. Performance was essentially stable at chance levels in the visuospatial-memory task, but was reliably better than chance ($z = 1.98$ or greater, all $p < 0.05$,) on the spatial-memory task, although accuracy did generally decline even on this task as it became more difficult. That is, the monkeys were able to perform the task that required only memory for “where”, as in Experiment 3, but not the task that required memory for “what was where.”

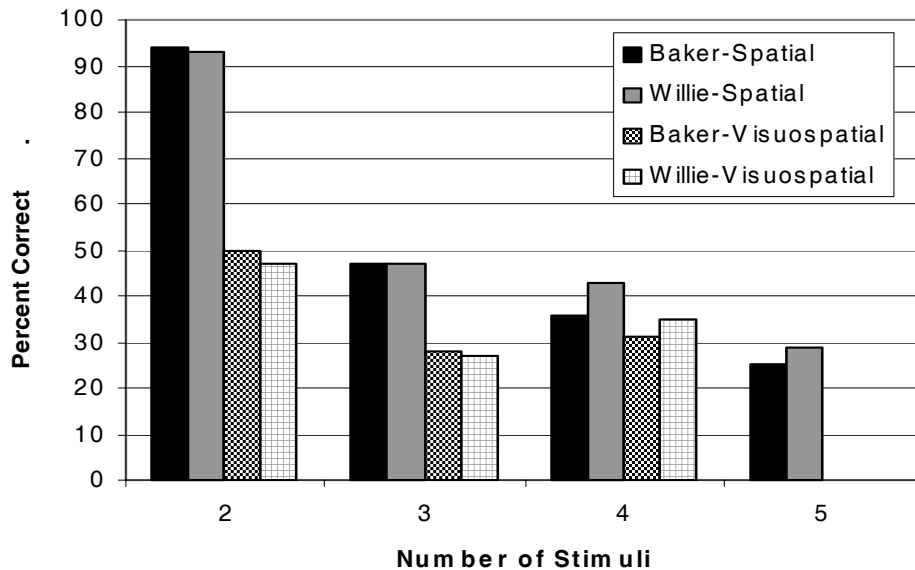


Figure 4. Experiment 4 results. Accuracy (percent correct) as a function of task and the number of boxes available. Chance was 50% with 2 boxes, 33% with 3 boxes, 25% for 4 boxes, and 20% for 5 boxes. The 5-box condition was only used with the spatial-memory task.

General Discussion

In previous studies (reported by Washburn & Gullledge, 2002), we have found that rhesus monkeys and humans show reliably different patterns of visuospatial memory performance on a computerized version of the Concentration task. In those previous experiments, we found that this difference in performance is not a failure by the monkeys to understand the basic nature of the Concentration task. That is, the animals appear to be trying to find the matching pairs of stimuli, but nevertheless manifest performance that is significantly worse than chance (as in Experiment 1 of the present report) across difficulty levels.

In the present series of experiments we have attempted to determine whether this performance pattern on the Concentration task—and specifically whether the preponderance of perseverative errors that are made by rhesus monkeys but seldom by college students—reflects a failure of visual memory (“memory for what was seen”), spatial memory (“memory for where was visited”), or the visuospatial coordination of memory codes (“memory for what was where”). We found that the perseverative errors in the Concentration task were not eliminated when we reduced the interference in remembering “what is where” by using problem-unique stimuli (Experiment 1). We further attempted to test the

limits of visual, spatial, and visuospatial memory by testing the monkeys with tests designed to capture only elements of the demands in the Concentration task. In a visual memory task, we found that the monkeys could accurately remember which of up-to-four images had been seen (Experiment 2), as is also suggested by previous results from the serial-probe recognition paradigm (e.g., Sands et al., 1984; Smith et al., 1998; Wright et al., 1984; Wright & Watkins, 1987). Not only could the monkeys perform well on this test of purely visual memory (meaning that there was no “memory for where” component), but they also performed significantly better than chance on a purely spatial memory task (i.e., no “memory for what” component; Experiments 3). However, their performance on the computerized version of the radial-arm maze task lagged reliably behind that characteristic of human adults, and was not as accurate as we had predicted. Consequently, we introduced two new tasks in Experiment 4: another spatial-memory task that required “memory for where” as in the Experiment 3 task; and another visuospatial-memory task that, like concentration, required memory for “what is where.” The monkeys performed well on the spatial task, but poorly on the visuospatial version. This pattern was consistent with our second of three hypotheses, discussed earlier, indicating that the monkeys do indeed have accurate spatial as well as visual memory, but that the coordination of these memory codes—remembering “what was where”—is poor for rhesus monkeys. That is, these data suggest that monkeys cannot perform as well as human adults (or even better than chance) on visuospatial tasks like concentration because they do not or cannot link precisely in memory the identity and the location of these stimuli. Monkeys perform at chance levels on concentration and similar visuospatial tasks despite the facts that (a) the animals apparently know that the game requires finding the location of matching images, (b) the animals are capable of discriminating and matching the stimuli, (c) the animals can remember what images they have seen, (d) the animals can remember where they have visited, and (e) the animals are not particularly affected by inter-problem interference. Rather, the monkeys appear not to perform well on any task that requires coordinated visual and spatial representations, even on the easiest conditions of that task.

These data are silent with respect to whether the problem experienced by the monkeys is an encoding issue, a retention issue, or a retrieval issue. That is, it may be that the monkeys do not or cannot integrate “what” and “where” cues in the memory code; alternatively, they may store an integrated representation but fail to retrieve “what was where” from this memory. We favor the former possibility. Because perseverative errors are, by definition, more likely for recently visited stimuli than those subject to the longest retention intervals, it seems unlikely that the cause of visuospatial memory failures is loss or interference of available integrated information. Rather it seems more likely that the nonhuman animals do not store “what” and “where” in an integrated and detailed object file, although there is evidence that the monkeys do attend simultaneously to both cue sources. We reported (Washburn & Gullledge, 2002) that the monkeys are unlikely to return within a problem to previously visited locations until at a pair of matching images had been viewed. That is, if a monkey’s first response reveals a picture of a dog, and the second card selected is of a train, the monkey is unlikely to return to either of these cards until either another dog or another train card (or some other pair) has been observed. This indicates that the animals are simultaneously tracking which

locations had been visited and which images had been seen within each problem. However, the animals (unlike people) do not seem to extract “what was where” information from these memories.

Several related reasons can be proposed to account for this species difference in visuospatial memory. Perhaps there are legitimate species differences in the capacity of the visuospatial sketchpad—to use Baddeley’s (1986, 1990, 1992) term for the process that supports working memory for visual or spatial information. This difference in capacity would be particularly evident under conditions in which memory of “what is where” is required, as the demands on memory are doubled relative to remembering only “what” or “where.” There is some evidence that the visuospatial memory capacity for nonhuman primates may be something around 4 items (e.g., Washburn & Gullledge, 1995), much less than the “seven, plus or minus two” typically associated with human short-term memory (Miller, 1956). However, estimates of the capacity of the visuospatial sketchpad (versus phonological working memory) in humans frequently run in the 4-item range (e.g., Luck & Vogel, 1997—but see Pickering, 2001, for larger estimates), a range comparable to that reported for monkeys and apes.

However, humans can use language to reduce the demands on visuospatial memory, specifically by transforming visual or spatial information into verbal codes that do permit the maintenance of 5-9 items (depending on item length). This system of verbal working memory, which Baddeley (1986) termed the articulatory or phonological loop, provides a tremendous economy for memory by humans. It is not clear whether rhesus monkeys have a comparable phonological memory system to complement the visuospatial sketchpad, and what the characteristics of such a system might be. However, it may be the case that humans outperform monkeys on the concentration because humans are uniquely capable of recoding the visual and spatial information into verbal codes (e.g., the horse is behind the third card). This possibility is being investigated in ongoing research.

Given these data, it appears that the perseverations that characterize monkeys’ concentration-task performance are precipitated by relatively accurate memory for what images have been seen and what locations have been visited, but poor memory for where each seen-image is located. Lacking veridical coordination of what and where, the monkeys tend to respond to stimulus locations that were recently visited. It is as if the monkeys are thinking, “I know I’ve seen the match for this stimulus, but I don’t remember where; however, I know I’ve been to this particular location a lot, so maybe that’s where the matching stimulus is located.” Under these circumstances, each time the monkeys repeat an error, it actually becomes more (rather than less) likely that the two (nonmatching) locations will be selected again.

The Concentration task, or more properly the game on which it was modeled, has been used to compare the visuospatial memory abilities of humans—children to adults, young to aged, normally developing or clinically defined (e.g., Arnold & Mills, 2001; Baker-Ward & Ornstein, 1988; Gellatly, Jones & Best, 1988; Portman, Feldstein et al., 1999; Schumann-Hengsteler, 1996a, 1996b). Because of this, and because of its nonverbal nature, the task would seem to be an ideal candidate for comparative investigations of memory. Indeed, it now has been used successfully with humans and with rhesus monkeys in a large series of experiments. Ironically, it appears possible that the attribute of the task that made it

ideal for comparative investigation of memory—its nonverbal nature—may have contributed to the reliable species difference that has been revealed: It may be the case that the human linguistic system makes a substantial and unique contribution to memory of what, where, and what-was-where information.

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