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Authors

Washburn, David A.
Gulledge, Jonathan P.

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A Species Difference in Visuospatial Memory in Adult Humans and Rhesus Monkeys: The Concentration Game

David A. Washburn and Jonathan P. Gullledge
Georgia State University, U.S.A.

One of the most familiar children's games (marketed under many names including the memory game, Concentration, and *Husker Du* also would seem to provide an excellent test of visuospatial memory. A computerized version of this game was written in which human adults or rhesus monkeys were required to find matching pairs of pictures by "flipping over" computer-generated images of cards. Finding one of the 2 to 6 pairs of images (color patches, line drawings, letters, etc.) caused the pictures to remain visible, but errors (mismatches) caused the images to be concealed again and thus required the participants to remember which images had been seen and where each was hidden. In a series of experiments, all participants were able to locate the pairs of stimuli, but monkeys were consistently and significantly worse than the human adults. Indeed, the monkeys frequently perseverated on errors, causing them to be worse than chance in many conditions, even after training. In the present manuscript, data are presented to suggest that this species difference does not simply reflect a limitation on the monkeys' knowledge of the "rules of the game."

One of the most familiar and popular of children's card games is a memory game called "Concentration" (also the matching game, *Husker Du*, and many other commercial names). The game typically requires a deck of cards in which each card has a picture on only one side, and in which there are exactly two cards printed with every picture. After the cards are shuffled and spread picture-side-down in an array, the players take turns flipping one card to reveal the image and then guessing (or remembering) where the matching card is located in the array. Matched pairs are removed from the array; however, if the matching card is not revealed the cards are returned picture-side-down to the original positions. Consequently, players must try to remember an increasingly long list of which images have been seen and where they are located.

The game can be played by people across the lifespan, from young children to elderly adults, and across demographic or diagnostic groups (e.g., nonreaders, children with mental retardation, adults with amnesia or communicative impairments, individuals from other cultures, or native languages, etc.). For these reasons, the game has been used in recent years to examine the characteristics of visuospatial memory in human children and adults (e.g., Eskritt, Lee & Donald, 2001; Knopf, 1989; Portman, et al., 1999). The Concentration game is one of the few memory tasks in which children are not predisposed to performing more poorly than adults by virtue of differences in vocabulary and articulation rate. Thus, the common report from parents that children may be as good or better

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than adults in the Concentration game has been supported empirically (Baker-Ward & Ornstein, 1988; Chagnon & McKelvie, 1992; Gellatly, Jones & Best, 1988), although other studies suggest that visuospatial memory on the Concentration task does improve into adulthood (Schumann-Hengseler, 1996a, b). The task has also been used to examine differences in visuospatial memory between people who use sign language (deaf and hearing signers) and nonsigners (Arnold & Mills, 2001; Arnold & Murray, 1998).

For these same reasons, it would seem that the Concentration game would also be an ideal task for the investigation of visuospatial memory across species. Nonhuman animals (at least those with acute visual abilities, like the monkeys used in the present study) should be able to match the pictorial stimuli hidden in a spatial array, and should not be automatically predisposed to perform poorly relative to humans due to differences in language, practice, or motivation. The spatial component of the task is similar to the kinds of foraging behavior that is natural for monkeys and other animals and that has been studied with a variety of other paradigms (e.g., McBurney, et al., 1997). Similarly, the matching component of the Concentration task is consistent with the skills of delayed matching-to-sample, sameness-difference, and other recognition paradigms for which the monkeys and apes have demonstrated competence (e.g., Smith, et al., 1998; Washburn & Astur, 1998). Other children's games have proven useful for studying species similarities and difference in memory performance (e.g., Washburn & Gullledge, 1995). Thus, we hypothesized that nonhuman primates would be able to master the basic demands of the Concentration game and that species differences, if any were observed, would reflect differences in the capacity of visuospatial memory between humans and nonhuman primates. It was further anticipated that these capacity differences, if they were revealed, would mirror the age-related differences reported in the literature for young children or elderly adults.

Experiment 1: Matching Colors

Method

Participants. Twenty undergraduate students (14 females) volunteered to participate in this experiment in exchange for class credit. The students ranged in age from 18 to 32 years (*Mean* = 20.23).

Two adult male rhesus monkeys (*Macaca mulatta*) were also tested in this study. The macaques (Abel and Baker, each 14-years-old at the time of Experiment 1) had previously been trained to manipulate a joystick so as to respond to computer-generated stimuli in accordance with task demands (Rumbaugh, et al., 1989; Washburn & Rumbaugh, 1992), and had been tested in a variety of studies prior to the present experiment (e.g., Smith, et al., 1998; Washburn & Astur, 1998; Washburn & Gullledge, 1995; Washburn, Hopkins, & Rumbaugh, 1989). The monkeys were not deprived of food or water for purposes of testing. Rather, they were tested in their home cages with continuous access to the apparatus and tasks, and thus could work or rest whenever they chose.

Apparatus. The monkeys were tested with the Language Research Center's computerized test system, which has been described in detail elsewhere (Rumbaugh et al., 1989; Washburn, Rumbaugh, & Richardson, 1992). Basically, the apparatus consisted of a standard 386-based computer and color monitor, an analog joystick, and a pellet dispenser (Gerbrands 5120). This apparatus was positioned so that the monkeys could reach out of their home cages to manipulate the joystick or to retrieve fruit-flavored chow pellets (P. J. Noyes, Lancaster, NH, U.S.A.) that were automatically dispensed using the dispenser interfaced with the computer via a relay box (Keithley PIO12 and ERA01). Auditory feedback was also presented to the monkeys through an external

speaker/amplifier.

Human participants were tested with comparable apparatus (i.e., individual computers and monitors, with responses made via joystick or keyboard), although no nutritive reinforcers were dispensed. The visual and auditory feedback that was provided to humans was identical to that delivered to the monkeys.

Task. A computerized version of the Concentration game was written for this experiment. On each trial of this task, a grid like the one in Figure 1 was presented on the screen. Each cell in the grid represented one potential position for a computer-graphic “card” in the task. Each active cell (i.e., those that contained cards) was identified with a large grey cross. Moving the cursor (a small white “+”) into an inactive cell did not result in any action; however, moving the cursor to an active card caused it to “flip over” to reveal a colored rectangle, whereupon the cursor returned to the middle of the grid. The cursor could then be moved to a second active cell, revealing the colored rectangle concealed beneath that card. If the two cards were identical (i.e., the colors matched), a tone was presented and 1 to 6 pellets were dispensed. In this case, the colored rectangles remained visible for the remainder of the trial (i.e., until all of the pairs had been located), although these cards were no longer responsive to the cursor. If however the cards did not match, a buzz was presented for 1 second before the cards returned to their original appearance (i.e., the back of the card, showing the grey cross, became visible). The cursor could then be moved to any active card, whether or not it had previously been revealed.

Each problem lasted until all of the pairs of stimuli had been located and matched. The task permitted between 1 and 8 pairs to be concealed on the screen, and the stimuli did not change positions during a problem. The stimulus colors and their locations were randomly selected for each new problem, however. Thus, each problem consisted of a number of trials (as many as were required to find the pairs of stimuli), and every response of each trial was recorded for subsequent analysis.

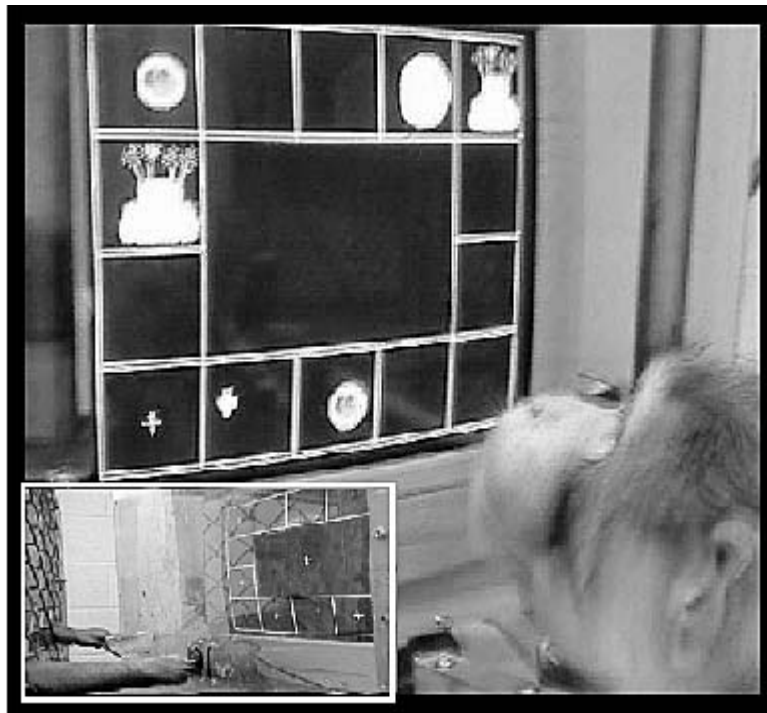


Figure 1. A monkey performing the Concentration task with three pairs of stimuli. Note the stimuli on the screen (a pair of birthday cakes, a pair of “go” buttons, and the monkey is trying to locate the matching image of Earth), which are typical of those used in Experiments 2, 3 and 4. Inset: Another angle, showing a monkey reaching through the mesh of his home cage to manipulate the joystick (right hand) and to retrieve pellets (left hand). For this picture, the cage has been pulled away from the screen more than was typical during testing.

Procedure. Each human participant was instructed regarding the nature of the task and subsequently completed 200 problems on the task. In each problem, a random number of pairs (between 2 and 6 pairs) was selected and assigned to locations

The two rhesus monkeys were initially trained with just one pair of stimuli for 50 problems. Although it was impossible to make an error in this condition (i.e., one could only turn-over cards in the pair), these problems were used to indicate the nature of the task to the monkeys. Subsequently, they completed 100 problems with two pairs of stimuli and 100 problems with four pairs. Finally, each monkey completed 5,000 problems in which the number of pairs (2 to 6) was randomized. These data were compared to those obtained from human participants under comparable conditions

Results

To determine the 95% confidence intervals around chance performance (given the skewed distribution that characterizes the number of errors at each level of difficulty), performance on the Concentration task was simulated with a computer program that picked cards randomly. The results from simulating the random solution to 1,000,000 problems at each difficulty level (i.e., number of pairs) are reflected in the present analyses.

Figure 2 shows that only the humans responded significantly ($p < 0.05$) better than chance on this task (i.e., their performance levels were observed in less than 5% of the random simulations). Monkeys made consistently more errors than did the humans, particularly with higher numbers of stimuli to be located. Generally and predictably, the number of errors did increase for both species as the number of pairs increased. The slopes of this relation (errors as a function of pairs) varied significantly between humans and monkeys, with the slope about 8 times steeper for monkeys than for humans.

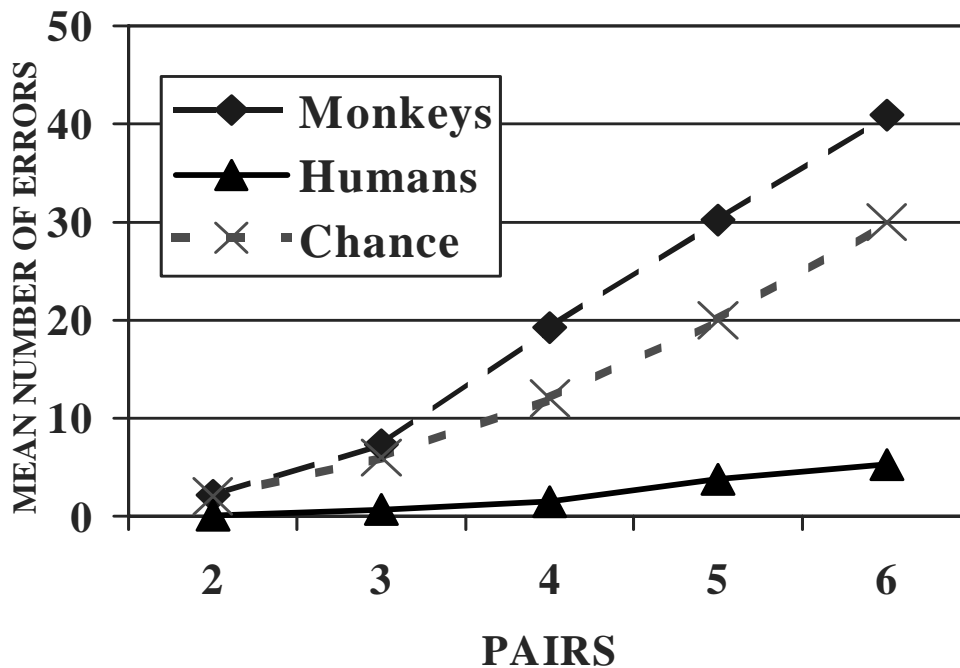


Figure 2. Mean number of errors in Experiment 1 as a function of species and number of pairs.

It is important to emphasize that the monkeys, like the human participants, successfully completed each of the problems that was presented to them. That is, they moved the cursor around the array of computer-graphic cards until all pairs of images had been located. Indeed, on many problems there was no discernable species difference in performance. With two pairs of stimuli, for example, humans tended to select the first two cards arbitrarily (revealing, for example, a red rectangle and a green rectangle); then, the human participant would select a third card and, generally, the “old” (previously revealed) card with the matching color; the final two cards would then be selected to complete the problem. Monkeys also completed many trials using this same strategy. However, the monkeys were much more likely than humans to perseverate on a particular error, and perseverated on this error for many more responses. Thus, there were trials in which monkeys picked two cards (e.g., card 1 = red, card 2 = green), then picked the third (e.g., card 3 = green) and first (red) cards, then card 1 (red) and card 2 (green), then card 1 (red) and card 3 (green), and then continued to make one or both of these errors for a dozen or more responses before revealing card 4 (red) and successfully matching both pairs of stimuli. As a consequence of these perseverative errors, the monkeys responded reliably worse than the human participants, and in fact responded significantly worse than chance under some conditions (see Figure 2). These perseverations are illustrated in Figure 3, which shows the frequency distribution of the dependent measure (number of errors per problem) for monkeys on three-pair problems. That is, Figure 3 reveals how often a particular number of errors would be expected by chance alone, and how often they were observed for the monkeys, on two-pair problems, three-pair problems, and so forth.

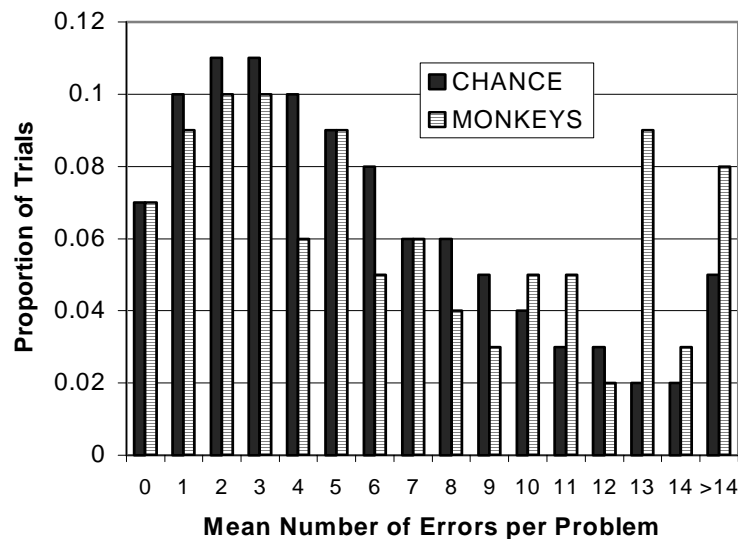


Figure 3. The distribution of errors on three-pair problems of Experiment 1, depicted both for two monkeys and for chance levels determined by simulation.

What is known about these perseverations? They did not follow a particular spatial pattern; that is, the monkeys did not show preferences for particular cells or locations within the matrix (e.g., the instances of perseveration did not involve

the same locations across problems). They were not more likely to reinforce spatial positions from previous trials. Neither did the perseverations appear to reflect proximity cues. That is, the monkeys were no more likely to repeat errors on spatially adjacent cards than for pairs of cards in other relative positions. The monkeys were not more likely to perseverate on certain pairs of colors to the exclusions of the others; indeed, the number of errors was approximately equal across the color combinations. Because the positions of stimuli were changed each problem, it seemed possible that perseverations would reflect instances in which stimulus positions were confused across problems; however, 58% of the perseverations involved stimulus positions unrelated to the location of either stimulus on the previous problem. Finally, although perseverative errors were more frequent and more robust as the number of pairs increased, they did not appear simply to reflect limits in the capacity of working memory (e.g., they did not reliably occur because the animal was trying to remember more than 4 stimulus-location associations). Perseverations were observed for 2-pair problems as well as for 6-pair problems, and there was no obvious pattern for their appearance as a function of how many stimuli had been observed (although this statement must be constrained by the discussion below).

In fact, only two variables seemed to be predictive of perseverative errors. The first variable is the obvious one: The probability of repeating an error increased with the number of times the error had already been repeated during the problem. The second variable is related, but more interesting: The probability of moving to a previously overturned stimulus differed as a function of whether a matching pair had or had not been revealed already in the trial. That is, the monkeys were highly unlikely to repeat an error when no matching pair had been revealed. For example, consider a 4-pair problem by Abel in which his first two responses were Card 1 (green) and Card 2 (white). His next two responses were to Card 13 (blue) and Card 4 (red). Abel was unlikely to revisit any of these card locations because no matching cards had been revealed. As another example, in the over-10,000 total problems completed by the monkeys in this experiment, only 20 times was an error made on the first trial repeated on the second trial. The probability of repeating an error increased dramatically once the participant had seen two matching stimuli somewhere on the screen. To illustrate, consider the following responses from a 4-pair problem performed by monkey Baker. His first two responses were to Card 3 (red) and Card 5 (yellow). His next two responses were to Card 8 (green) and Card 9 (red). Under these conditions, Baker was highly likely to revisit one of the four cards he had already overturned. On this particular trial, Baker moved next to Card 3 (red) and Card 9 (red) for the match; however, on other problems like this, an error might be made—or even a string of repeated errors before the match would be achieved. The major point is that the probability of a monkey revisiting an old stimulus when a pair had been revealed ($p = 0.72$) was greater than the probability of returning to an old stimulus if no match had been revealed ($p = 0.09$).

Discussion

Our interpretation of these data was that the monkeys (and, of course, the undergraduates) knew that the object in the task was to locate matching pairs of images, and that the animals were motivated to respond accordingly. The fact that

the monkeys (like humans) tended not to revisit old stimuli until two matching stimuli had been revealed indicates that the monkeys were trying to locate the matching pairs. For some reason, however, the monkeys were uniquely susceptible to occasional errors of perseveration, trials in which the same error or pair of errors got repeated many times. That is, the monkeys appeared not simply to be moving the cursor around randomly, but rather seemed to respond rather smartly except for these occasional and inexplicable occasions in which the animal got stuck. Ignoring these perseverative occasions, the monkeys' data look very similar (although still not quite as good) as those from humans—but of course there is no justification for removing these perseverations. That is, the perseverative errors are also a legitimate, if unexpected, part of the monkeys' behavioral response to the task.

Experiment 2: Matching Forms

Following Experiment 1, we conducted a series of studies designed to identify the source of these perseverations, to eliminate these perseverations, to train the monkeys to be more efficient in their responses, or at least to reveal the nature of the large and reliable species difference that is reflected in Figure 2. The first of these follow-up studies involved replacing the color patches with multichromatic pictures, line drawings, letters, and other form stimuli. The monkeys could certainly distinguish the color patches from one another, and would have responded near-perfectly on a matching-to-sample task with these colored rectangles as stimuli. However, it was hypothesized that the color-patches were too similar to one another to produce ideal representations in visuospatial memory, and that form stimuli that differed in color and shape would be easier to remember.

Method

To determine whether the patterns of performance observed in the previous study were limited to the monkeys Abel and Baker, four additional rhesus monkeys (males, age range 6 to 16 at the time of the study) were also tested in Experiment 2 ($n = 6$). Like the monkeys from the prior study, these animals had been trained to respond to computerized tasks by manipulating a joystick, and had participated in numerous studies previous to the present research. None of the six monkeys was deprived of food or water for purposes of testing, and each was allowed to work on the test (or to refrain from working) on an ad lib.

The monkeys were tested on a new version of the Concentration task. The task was identical to the description in Experiment 1 except that multicolored pictures or line drawings were used as stimuli (see Figure 1 for samples). Two to six pairs of these stimuli would be concealed beneath computer-graphic cards on each problem. The same library of eight pictures was used for each block of approximately 1,000 problems, although the specific pictures that were selected from the library as well as the location of the cards that concealed each image were randomized for every problem.

The monkeys also were tested on a delayed matching-to-sample (DMTS) task using the stimuli employed in this experiment. This is a task on which each monkey was highly experienced from prior training and testing. The purpose of the present DMTS testing was to verify that the monkeys could indeed discriminate and remember the images being used here. Each DMTS trial began with the cursor presented midscreen and a randomly selected sample stimulus presented in random position on the screen. When the cursor was brought into contact with the sample, the sample disappeared for a 10 s retention interval, after which the sample stimulus and a randomly chosen nonmatching stimulus were presented on the screen in random but nonoverlapping positions. A response was reinforced as correct if the monkey brought the cursor into contact with the sample stimulus, but a 5 s buzz followed responses to the nonmatching comparison stimulus. Each monkey

completed 1,000 of these DMTS trials.

Each of the monkeys completed a minimum of 12,000 problems on this version of the Concentration task. For the present analyses, the first 1,000 problems were examined for evidence of transfer from the previous version. The most recent 1,000 problems were also analyzed for evidence of learning. In addition, 32 human undergraduates each completed 100 problems on the Concentration task with the stimuli shown in Figure 1. These students (*Mean* age = 20.28; 22 females) volunteered to participate in exchange for course credit.

Results

The results of this experiment were comparable in every way to the data reported for Experiment 1. The number of errors produced by humans and by monkeys generally increased as the number of pairs increased. Monkeys produced consistently more errors than humans, and in fact consistently more errors than were produced by chance simulations. These means are evident in Figure 4. The monkeys were occasionally victimized by perseverative errors and the frequency distributions of errors-per-trial as a function of number-of-pairs were similar to those observed in Experiment 1.

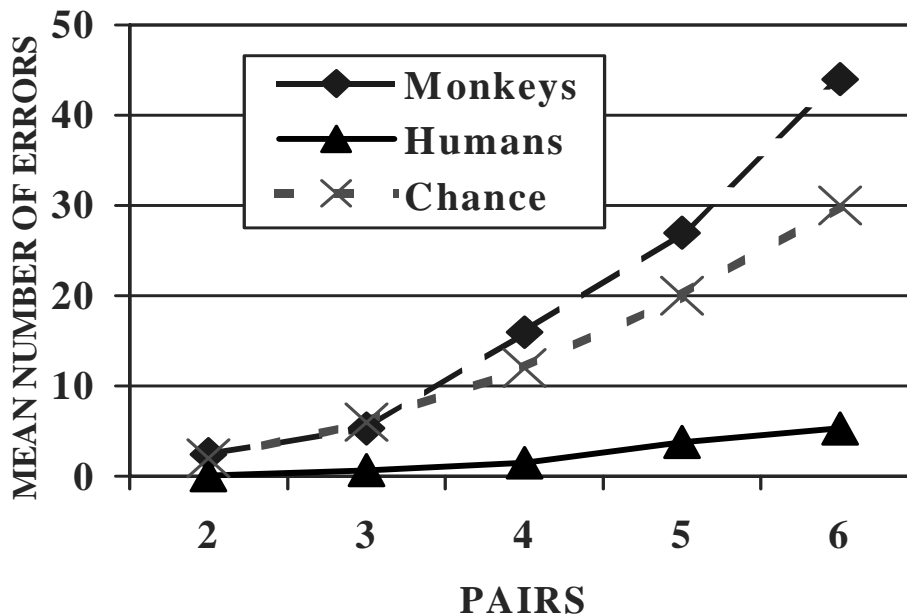


Figure 4. Mean number of errors in Experiment 2 as a function of species and number of pairs.

The monkeys' performance did not differ significantly between the first 1,000 trials and the last 1,000 trials of testing ($p > 0.10$). Rather, performance was stable and asymptotic across the corpus of problems presented to the animals.

To verify that the monkeys could indeed discriminate the images used in this study, each animal completed 1,000 DMTS trials using the stimuli. Recognition accuracy was high (*Mean* = 0.92) across these trials, including on the first presentation of each stimulus in the DMTS paradigm (*Mean* = 0.90).

Discussion

Clearly, changing the nature of the stimuli from color-patches to images did not improve the monkeys' performance on the Concentration task, even though accuracy levels on the DMTS leave no doubt that the monkeys could discriminate and remember the stimuli. Because the monkeys were performing at or near chance levels even in the easiest test condition (2-pair problems), it is difficult to ascertain conclusively whether these reliable patterns of performance observed on the Concentration task reflect limitations in monkey visual memory, limitations in monkey spatial memory, limitations in the coordination of these memory codes, failures of strategy and planning, or even a lack of basic understanding of the nature and goal of the Concentration task. With respect to this latter possibility, it did appear again that the monkeys were trying to locate matching pairs of images, as evidenced by the number of trials they completed efficiently and by the improbability of error-repetition prior to the discovery of a matching pair. However, the accuracy of the monkeys' responses still lagged well behind their own DMTS performance, behind humans' Concentration performance, and even behind that which would be expected by chance alone.

Experiment 3: The Three-Card Task

Of course, it would be meaningless to compare humans and monkeys on the Concentration task with only one pair of stimuli, as it is impossible to make an error under this condition. However, we believed that it might be informative to provide the monkeys with a trial condition easier than the 2-pair problem so as to determine empirically whether in fact the monkeys understood the nature of the task. In Experiment 3, humans and monkeys were tested with a three-card version of the Concentration task in which each problem consisted of one matching pair of cards and an additional (nonmatching) foil card.

Method

The monkeys from Experiment 2 were again tested ($n = 6$). Each problem began with the cursor located in the middle of the screen. Three cards appeared in random locations in the grid around the cursor. As with previous versions, touching a card location caused it to "flip over" and to reveal an image. Touching a second card revealed either a matching image or a nonmatching image. If the matching image was located, a reinforcer was dispensed and the trial ended; otherwise, the cards returned to their original appearance and the problem continued. Each monkey completed 300 problems of this three-card task.

With just one pair of stimuli (but three cards per problem), it is a straightforward matter to determine from simulations the frequency with which the matching images would be found without error, with one error, with two errors, and so forth. The expected distribution of errors according to chance is graphed in Figure 5. With this distribution, different predictions can be made to determine whether the monkeys were indeed trying to find pairs of stimuli or were just responding randomly. Of course, problems ended with 0 errors must always be due to chance, and should account for 33% of the problems. Only 9% of the problems would be expected to have more than five errors by chance alone. The most important predictions for this experiment pertain to problems with one error, however. If the monkeys are responding randomly, one would expect 22% of their three-stimulus problems to be completed with exactly one error. Conversely, if the monkeys were not responding randomly but were in fact trying to find matching stimuli, then the percentage of problems with exactly one error should be significantly in excess of 22%. Indeed, one would expect virtually all of humans' three-stimulus problems to be completed with either zero or one error.

Results

By chance alone, one would expect an average of 2 errors on the three-card Concentration problems. The six monkeys completed 300 problems each with an average of 2.53 errors per problem ($SD = 0.49$). This might indicate, as might the results from previous experiments, that the monkeys were responding randomly on the task. However, the distribution of errors produced by the monkeys differed significantly from that expected by chance, as displayed in Figure 5. Most importantly, 32% of the problems were completed by the monkeys with exactly one error. In 1,000,000 simulations of the three-card task (each simulation producing 300 problems), 32% or more problems with only one error occurred on only 100 of the simulations. Thus, it is highly unlikely ($p = 0.0001$) that as many as 32% of the problems could have been completed with one error by chance alone. That is, the monkeys produced significantly more one-error problems than would be expected by chance alone ($p < 0.001$). No other proportion displayed in Figure 5 differed reliably from chance ($p > 0.10$)

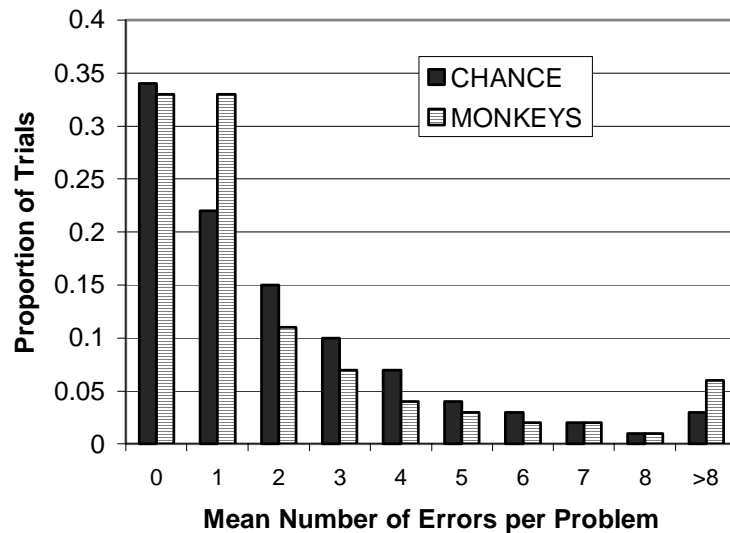


Figure 5. The distribution of errors in Experiment 3, depicted both for six monkeys and for chance levels determined by simulation.

Discussion

Previous experiments suggested that the monkeys were trying to find pairs of stimuli, but were (for unknown reasons) inefficient at doing so. By simplifying the predictions pertaining to error patterns, the present experiment indicated conclusively that the monkeys did indeed learn that the object of the game was to find matching images, and that they were trying to behave accordingly. As in previous experiments, however, the occasional occurrence of repeated errors (resulting in more trials than expected at relatively high error levels) produced overall performance that was poor.

Experiment 4: Training Efficient Performance

Summarizing from the first three experiments, we are left with a dilemma. The data indicate that the monkeys are indeed trying to find matching stimuli concealed in the arrays of the Concentration task in its various versions. However, they perform so poorly at the task that performance would actually be improved on average if the animals simply closed their eyes and moved the cursor randomly around the screen! It seems clear from Experiment 3 that the monkeys do understand that the task requires finding matching stimuli, and from all of these data that performance is asymptotic and would not benefit simply by exposure to additional problems. Consequently, Experiment 4 was designed to determine whether the monkey could be trained to eliminate perseverative errors and to improve performance.

Schumann-Hengsteler (1996) described a task analysis of the Concentration game, noting that performance requires “what” memory, “where” memory, and also strategy that includes the avoidance of redundancy. Young children are generally more redundant than adults in their attention and search strategies (Miller, 1990; Wellman, 1985); that is, children are more likely to repeat erroneous responses. In at least one study, children were explicitly and effectively trained to use a nonredundant strategy in the Concentration game by blocking the inefficient responses (Gellatly et al., 1988). Consequently, we attempted both an extinction approach and a penalty approach to discouraging perseverations.

Method

Two of the monkeys from Experiment 3 (Abel and Baker) were assigned to the penalty-approach group. Two other monkeys (Willie and Hank) were assigned to the extinction-approach group. For the penalty version of training, the Concentration task was modified to allow a timeout to follow each error. The timeout period varied from 1 to 60 s, and was titrated according to the number of errors observed on the current problem. Thus, each error caused the timeout period, during which a buzz sounded and no responses could be made, to increase by 1 s. In this way, the animals were penalized for perseverating on errors (or, more generally, for making errors). The timeout duration was reset to 1 s with each new problem.

For the extinction-approach group, the Concentration task was modified to disallow the selection of a previous error. (This approach is termed “extinction” for lack of a better shorthand, and in deference to the fact that attempts to repeat an error were not subject to the secondary reward of having the card overturn.) If a monkey tried to pick a pair of cards that had already been revealed as an error, the card would not “flip over” when touched by the cursor, and thus the monkey would have to move to a different card. For example, if on Trial 1 the monkey picked card 1 (a picture of a cactus) and card 2 (a football), the task would not allow these two cards to be flipped together again on Trial 2 or any other trial in that problem. If on Trial 2 the monkey picked card 2, then card 1 would become unresponsive to the cursor and the monkey would have to pick a different (and possibly correct) card.

All four monkeys were trained on their respective versions of Concentration for 2,000 problems. Subsequently, an additional 1,000 problems of Concentration were administered using the software from Experiment 2 (i.e., without the training intervention) to determine whether the training would generalize to conditions in which the task allowed perseverations without additional penalty. Two or three pairs of cards were used in each problem, both for the training phase and the posttest phase.

Results

Penalty-Approach. Abel and Baker produced fewer trials each day during training than in Experiment 2 or the Experiment 4 posttest. In the posttest for example, these monkeys each averaged about 214 problems per day (or about 1,500 trials each day for each monkey). During training, they completed fewer than 150 problems (about 900 trials) per day. This reflects the fact that training problems took longer to complete because of the longer timeout periods, as well as the fact that Abel and Baker were likely to stop working after several long penalties. Perhaps for this latter reason, or perhaps because the timeout introduced forgetting that attenuated the likelihood of perseveration, performance did improve when the training task was introduced. However, there was no general trend toward improvement with additional practice (Figure 6). As can be seen in the figure, however, performance returned to baseline levels during the posttest.

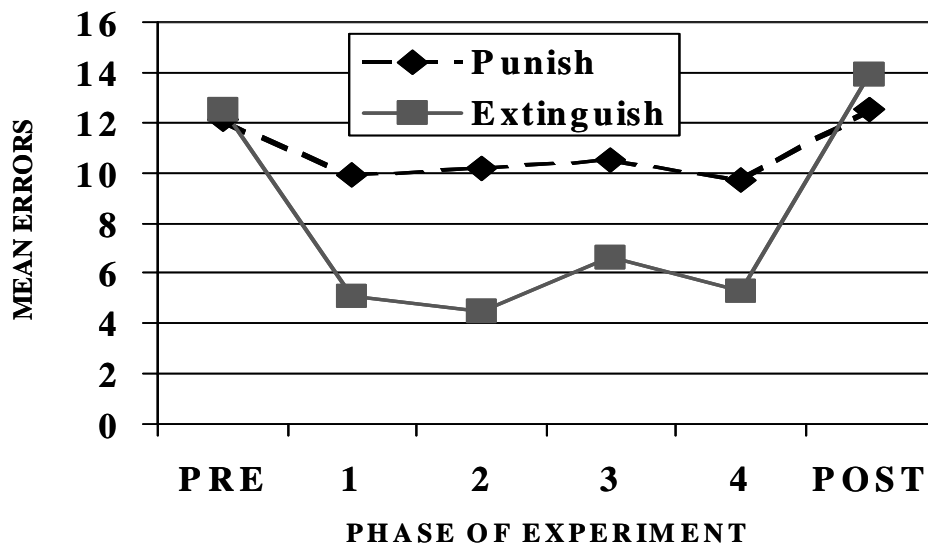


Figure 6. Experiment 4. Mean number of errors on 2-pair and 3-pair problems as a function of group and experimental phase (including block of 500 training trials)

Extinction-Approach. Hank and Willie also produced fewer trials during training than during previous tests or the present posttest. These monkeys typically average about 1,300 Concentration trials (or about 140 problems) each day, as in the posttest of this study. During training, only about 1,050 trials per day were produced by each monkey, although this actually resulted in more problems per day (*Mean* = 191). This increase in the number of daily problems, even as the number of daily trials dropped, suggests that performance was greatly improved during training. This effect can also be seen in Figure 6. As with the other group, however, there was no evidence of a trend in performance across blocks of problems, and performance returned to its pretraining levels during the posttest.

Discussion

Two strategies were employed to train the monkeys not to perseverate on

errors. Either by penalizing or by prohibiting perseverative errors, performance on the task was improved. However, these improvements were artifactual. In one condition, the improvements may have resulted merely from the impossibility of making certain kinds of errors. In the other, the improvements may have reflected (ironically) benefits of forgetting—longer retention intervals imposed by the timeouts may have reduced the activation of spatial locations that were leading to perseverations. In either case, the posttest data indicate that the monkeys did not learn to avoid perseverative errors. When the constraints on responding were removed and the monkeys were tested on the basic Concentration task, accuracy returned to levels typical of the previous experiments, including those perseverations that cause performance to be comparable to or worse than chance. Although one might always claim that more training or different types of training could make a difference, there are no indications in the current data that the monkeys were improving in their ability to avoid perseverative errors.

General Discussion

In four experiments, rhesus monkeys were tested on a visuospatial memory task, inspired by a simple and popular children's game. As hypothesized, the monkeys did learn to play the game, as the data from these studies suggest that the animals were indeed trying to find matching stimuli. Across the four experiments, the monkeys completed over 100,000 problems (over one million trials) of this Concentration task under various conditions, indicating that they generally liked the task and worked successfully at it. Despite this, and much to our surprise, the monkeys were not efficient at locating the hidden stimulus matches. From the very first block of problems until the most recent, the monkeys' performance was comparable to or even worse than would be expected by chance alone. Simulation studies revealed that the monkeys were not in fact responding randomly; however, had they done so, performance would actually have improved! This is because the monkeys were susceptible to perseverative errors—repeated commission of the same error or small subset of errors in a problem—that were as debilitating as they were inexplicable. It was not apparent why the monkeys would occasionally perseverate on an error, resulting in dozens or even hundreds of errors on a single problem. The perseverations were not obviously related to particular stimuli or stimulus locations, to sequences of stimuli across problems, or even to particular levels of task complexity (i.e., perseverations were observed even on the easiest task conditions, although they were more frequent and more severe with 6-pair problems than 2-pair problems). This tendency to perseverate on errors was not reduced as a result of extensive practice on the task, or as a result of specific efforts to extinguish or penalize error repetitions. The patterns of performance observed here were reliable across animals and across experiments. Thus, the perseverative errors appear to reflect a true limitation in the visuospatial memory skills of rhesus monkeys, and the performance differences reported here between the nonhuman primates and humans would seem to reflect true and meaningful species differences in visuospatial memory that should be subject to further investigation.

There were good reasons to anticipate that the monkeys would be able to perform this task well. As was discussed above, children can play the Concentration game occasionally as well as adults. Rhesus monkeys show good visuospatial

memory performance on other tasks, such as the DMTS test used in Experiment 2. Additionally, some bird species are famously adept at remembering what foods are cached in various locations (Clayton & Dickinson, 1998; Clayton, Yu, & Dickinson, 2001; but see Kraemer, Mazmanian, & Roberts, 1987 for limits on pigeon memory of “what is where”). In a similarly naturalistic experiment, Menzel (1999) also reported impressive recall of “what” and “where” information by a language-trained chimpanzee.

Conversely, and as was stated already, there are several reasons why the animals might perform poorly on this task. Poor performance might reflect a lack of understanding about the purpose or rules of the task. We believe that the present data controvert this possibility, and that the monkeys were indeed trying to find matching stimuli in each of the experiments. However, poor performance might also reflect limitations in visual memory (remembering what was seen), limitations in spatial memory (remembering which locations had been visited), or the coordination of the two memory modalities. That is, it seems reasonable that rhesus monkeys are incapable of maintaining an accurate problem-by-problem index of “what was seen and where.” Rather, they appear to respond to stimulus locations on the basis of activation or familiarity, such that the more often they have responded recently to a particular location or image, the more likely they are to return to that location with a subsequent response.

Of course, the animals must retain some, albeit limited or imperfect, information about the images that have been revealed and the cards that have been visited on each problem. “What was seen and where” are clearly relevant to responding, as the monkeys generally do not begin to revisit old cards until a matching pair has been revealed. Once that happens, however, where the monkeys visit appears to be guided largely by “which cards have been overturned recently that potentially contain the match?” Thus, the perseverations engender a maladaptive cycle: Rather than acting punitively to discourage further visits to the same stimulus locations (after all, each error takes time and effort that is unreinforced, even without the manipulations implemented in Experiment 4), each perseveration serves to make the respective cards/images more active and more likely to be paired again. Only when the monkey eventually walks away from the task for a few minutes (perhaps due to frustration) does the activation seem to fade, allowing the animal to find the pairs efficiently.

This description leaves unanswered the important question of why the perseverations occur, or more specifically why they occur only occasionally. If one accepts that the monkeys do indeed understand the nature of the task, then the perseverative errors must reflect something real about nonhuman primate cognition. It seems unlikely that they reflect mere wanes in motivation, because the monkeys work *ad libitum* and can stop working whenever they are unmotivated (as they tended to do in the training phases of Experiment 4). In other tasks, we have seen the monkeys respond in less-than-optimal ways that can only be described as “play” (Washburn, 2001). On maze tasks, for example, the monkeys have been observed to delay capturing the target, even after solving the two-dimensional maze, until they have explored the maze more fully. That pattern seems very different than the one reported here for the Concentration task, making it doubtful that the monkeys are intentionally perseverating on errors just to play the task. Rather, we assume that the species difference in Concentration performance on the

Concentration task reported here reveals something meaningful about the capacity, code, or control of visuospatial working memory across primate species. Exactly what these patterns mean, however, must be the subject of further investigation.

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