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Monitoring Spatial Transpositions by Bonobos (*Pan paniscus*) and Chimpanzees (*P. troglodytes*)

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Two bonobos (*Pan paniscus*) and three chimpanzees (*P. troglodytes*) monitored spatial transpositions, or the simultaneous movement of multiple items in an array, so as to select a specific item from the array. In the initial condition of Experiment 1, food reward was hidden beneath one of four cups, and the apes were required to select the cup containing the reward in order to receive it. In the second condition, the test board on which the cups were located was rotated 180 degrees after placement of the food reward. In the third condition, two of the three cups switched locations with one another after placement of the food reward. All five apes performed at very high levels for these conditions. Experiment 2 was a computerized simulation of the tasks with the cups in which the apes had to track one of four simultaneously moving stimuli on a computer monitor. Two of the three apes that were tested performed at a very high level for this computerized task. Therefore, members of the genus *Pan* can perform complex feats of spatial monitoring such as transpositions both in real world contexts and in computerized tests.

Spatial cognition allows organisms to keep track of, or spatially monitor, the position of an item as it moves through space. When multiple items move within the visual field during a discrimination task (a spatial transposition), the organism has to monitor the movement of relevant items while disregarding other irrelevant object movements. Whereas some forms of spatial monitoring can be done perceptually by noting where various specific items are at separate points in time, spatial monitoring also may be dependent upon an individual’s inference regarding where items are located after they move when the subject does not see them in their new positions (Sophian, 1984, 1986).

The ability to track an item that has been hidden behind or inside a masking agent prior to its movement requires a sense of object permanence, particularly if it is demonstrated that the monitoring of a given masking agent occurs because an organism is interested in the hidden item under or behind the masking agent. Object permanence is the recognition that an

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object in one's environment is independent of one's own actions and perspectives and will continue to exist even when it cannot be viewed directly (Piaget, 1954). Piaget (1954) demonstrated that children younger than 2.5 years of age reconstruct series of invisible displacements, or movements of a single object in situations in which the object itself cannot be seen but the container in which the object is hidden can be seen. However, monitoring spatial transpositions in which one of multiple simultaneously moving items contains a desired object remains difficult for children younger than 4.5 years of age (Sophian, 1986).

Typically, observations of object permanence in nonhuman animals have employed some variation of a method used by Piaget (1954) in which the ultimate demonstration occurs when an animal tracks the movement of a hidden object to only those positions in which it possibly could be located. For example, after being hidden under one cup, that cup may move behind a second cup, where the hidden item is surreptitiously moved from the first cup to the second. If the subject tracks the original cup to its final location but does not find the hidden item there, it should only look next at the cup to which the item had been transferred. To date, various species of birds (Pepperberg & Funk, 1990; Pollok, Prior, & Güntürkün, 2000), cats (Dumas, 2000), dogs (Gagnon & Doré, 1993; Pasnak, Kurkjian, & Triana, 1988), monkeys (Schino, Spinozzi, & Berlinguer, 1990), a gorilla (Natale, Antinucci, Spinozzi, & PotΞ, 1986), orangutans (de Blois, Novak, & Bond, 1999), and a chimpanzee (Wood, Moriarty, Gardner, & Gardner, 1980) have passed various tests of object permanence such as the one described above (see Tomasello & Call, 1997, for a review). However, the methodology used in many of these studies has been questioned on the ground that it may allow animals to use simpler strategies (Gagnon & Doré, 1993). For example, in some studies, the animal may respond to only the second container that has been manipulated. To control for this possibility, de Blois et al. (1999) presented trials in which there was no transfer of the object from its original box and reported that orangutans and monkeys solved such problems. Natale et al. (1986) presented trials in which the container holding the hidden food was not moved, but an adjacent container was manipulated. A Japanese macaque made errors in selecting the empty manipulated container, but a gorilla made no errors in this test.

In experiments involving spatial transpositions multiple items move at one time eliminating any bias toward particular objects that have moved. Additionally, memory for the last location at which an object was seen is not sufficient for finding a hidden object that has undergone a spatial transposition. There also must be an understanding of the physical nature of objects and containers and how they relate through movement of the latter while holding the former. Therefore, in addition to providing information about the representational aspects of spatial cognition in nonhuman animals, an investigation of the monitoring of spatial transpositions also may provide some insight into object permanence in nonhuman animals. This insight will not be that of determining whether a nonhuman animal “passes” a human test of object permanence, but will be focused on how the animal finds a hidden object (Shettleworth, 1998). Spatial transposition tasks are not the same as object permanence tasks. Object permanence tasks are focused on whether a subject understands that the movement of a container changes the possibilities for where an item hidden in that container may end up being located. Spatial transposition tasks are focused on the extent to which subjects can attend to relevant movements of target containers (typically, those containing the desired reward) while discounting irrelevant, simultaneous movements of other containers (the “empty” ones). Of course, monitoring the movement of a masking agent through a spatial transposition does not necessarily indicate that an organism understands the permanence of an object hidden within that masking agent (i.e., the accurate monitoring of spatial transpositions need not rely on some belief about the continued existence of the hidden item). A necessary component of adequate testing of object permanence is that the target object elicits search behavior by the subject because of its incentive properties, rather than on the basis of some other cue (Dumas, 2000). Therefore, first trial performance is important in such tests of spatial monitoring as is an expectation that the subject’s search strategy is based on an attempt to find the hidden item.

Why would monitoring spatial transpositions be beneficial to nonhuman animals? To give one example from the behavior of wild apes, consider cooperative hunting of monkeys by chimpanzees (Boesch, 1994; Boesch & Boesch, 1989). As multiple individuals move through the trees and a monkey attempts to escape, each “hunter” has to maintain a representation of the location and monitor the movement of the monkey as it passes behind thick foliage. At the same time, the monkey’s position cannot be confused with the position of other apes, or the hunt will be unsuccessful. Consider further the importance of monitoring the movement of a potential predator through dense grass or vegetation as it temporarily moves in and out of view. Additionally, the ability to monitor spatial transpositions would be useful when traveling with a social group. Separation from the group for periods of time would not be detrimental to an individual, if that individual could monitor the disruption of underbrush on the ground or the movement of limbs in the trees, and recognize that movement as being the result of the travel of other members of the group. The same is true of the separation between mother and infant that occurs as the infant becomes more independent. Both mother and infant can represent the movement of the other even when out of view.

In the experiments presented in this paper, individual apes were observed in two situations. The first was a real-world evaluation of the apes’ monitoring of spatial transpositions. A highly preferred food was hidden beneath one of multiple containers, and then multiple containers were moved simultaneously. The apes selected one of the containers and received the preferred food if it was hidden under that container. Apes spontaneously indicate the larger of two food quantities with very little task experience necessary (Beran, 2001; Call, 2000; Rumbaugh, Savage-Rumbaugh, & Hegel, 1987), and they have difficulty indicating a smaller quantity over a larger quantity (Boysen & Berntson, 1995). Therefore, apes indicate locations that contain consumable items, and it is assumed that the apes in the present study will indicate where they believe the food to be located. To correctly select the container with the preferred food requires that the apes recognize that the food item will move with its container even when they do not visually witness the movement of that food. The apes will have to recognize that the food moves with the container rather than being constrained to the location in space at which they initially had seen it being placed.

In the second experiment, spatial transpositions occurred on a computer monitor. The apes viewed a red square move into one of four boxes with each box positioned in a different corner of the screen. All four boxes then moved simultaneously in a clockwise direction, and the apes had to select the final location of the box containing the red square. In the computerized tasks, we are mainly interested in the subjects' ability to track the movement of individual items during spatial transpositions. Nonhuman primates perform better on computerized tasks of learning, matching, and memory when the stimuli move on the computer monitor (Washburn, 1993; Washburn, Hopkins, & Rumbaugh, 1989; Washburn & Putney, 1998). Additionally, nonhuman primates have been shown to track the movement of single items on a computer screen in a variety of tasks, the main example of which is tracking the movement of a subject-controlled cursor on the monitor and the tracking of a given stimulus to be contacted with that cursor (Rumbaugh, Richardson, Washburn, Savage-Rumbaugh, & Hopkins, 1989; Washburn, Hopkins, & Rumbaugh, 1990; Washburn & Rumbaugh, 1992). Adult humans have little difficulty tracking multiple moving items on a computer monitor provided the number of items is not too large (Scholl & Pylyshyn, 1999; Sears & Pylyshyn, 2000). However, few experiments have examined nonhuman animal tracking of the movement of multiple, identical items on a computer screen when the task involves the subsequent selection of one of those items.

The first question addressed in these experiments is whether chimpanzees and bonobos monitor spatial transpositions. In addition, real world and computerized tests of spatial monitoring will provide data regarding the effects of different testing mediums on the spatial cognition and representation abilities of these apes. Therefore, the second question is whether the medium through which spatial transpositions occur affects the performance of the apes. Additionally, as already noted, success in Experiment 1 (and perhaps in Experiment 2) would allow some interpretation of the subjects' recognition of object permanence.

Experiment 1

The first experiment is based on research conducted by Sophian (1984, 1986) with human children, in which items were hidden in one of several containers and then multiple containers were moved at the same time. Sophian (1986) stated that these problems required that the children infer what happens to an object based on the movement of its container. Additionally, if it is assumed that the child is trying to obtain the hidden item, then the task would require an understanding of object permanence.

In the initial condition in the current experiment, a food item was hidden beneath one of multiple identical cups, and the apes then selected one of the cups after a short delay. Note that this manipulation is similar to the research on delayed reaction and memory conducted by researchers in the early 1900s with nonhuman primates (Köhler, 1925; Tinklepaugh, 1928, 1932; Yerkes & Yerkes, 1928). For example, Tinklepaugh (1928) presented monkeys with two containers, one of which had a piece of food placed into it. The monkeys were successful in remembering the correct location of the food when different types of containers were used and when identical containers were used. In later experiments (Tinklepaugh, 1932), chimpanzees also performed delayed-reaction tasks successfully. Additionally, the chimpanzees and monkeys were shown hidden items placed under one of a pair of containers in multiple rooms, and they were successful in retrieving the items from each room.

In delayed reaction experiments, the food items remained in their original location. However, in some conditions in the present experiment, the containers were moved in the presence of the apes. Tinklepaugh (1932) reported one experiment in which monkeys viewed food being placed into one of three containers of different sizes, shapes, and colors. Then, in view of the monkeys, the containers were shifted in position. However, the monkeys did not take into account the movement of the containers, and they continued to respond on the basis of the original location of the food rather than on the basis of the container holding the food. The present experiment is designed to address the effects of such spatial transpositions on the performance of chimpanzees and bonobos in selecting the container in which food was placed.

Method

Subjects. Three chimpanzees (*Pan troglodytes*) and two bonobos (*P. paniscus*) were observed in this experiment. The chimpanzees were Lana (female, 29 years of age), Sherman (male, 26 years of age), and Panzee (female, 14 years of age). These chimpanzees had been involved in cognitive research examining such topics as language acquisition, numerical competence, memory, and delay of gratification (Beran, Pate, Richardson, & Rumbaugh, 2000; Beran, Savage-Rumbaugh, Brakke, Kelley, & Rumbaugh, 1998; Menzel, 1999; Rumbaugh, 1977; Rumbaugh, Hopkins, Washburn, & Savage-Rumbaugh, 1989; Savage-Rumbaugh, 1986).

The two bonobos were Kanzi (male, 19 years of age) and Panbanisha (female, 14 years of age). These bonobos had been involved in cognitive research concerned with language acquisition and tool making (Savage-Rumbaugh & Lewin, 1994; Savage-Rumbaugh, Murphy, Sevcik, Brakke, Williams, & Rumbaugh, 1993).

Apparatus. Opaque cups (tumblers) were placed upside-down onto a tray such that they were in a row and were separated from each other by approximately 12 cm. The cups were visually matched so as to be as close to identical as possible. The tray also contained no discernible features that distinguished different parts of it. The tray could be pushed forward so that the ape could reach a finger through the cage wire and touch one of the cups. All of the apes had prior experience reaching through the cage wire and touching items that they wanted to receive from multi-item arrays.

Procedure. Each ape was tested individually. The ape was seated inside its cage across from the experimenter who was on the outside of the cage. Between the ape and the experimenter was the tray with the opaque cups. During the stable location condition, each ape was presented with four cups placed in a row on the tray. When the ape was attending to the tray and the cups, the experimenter manually presented a piece of food (a marshmallow or other candy treat). The experimenter then lifted each cup in succession from left to right and placed the hand containing the food under each cup for approximately 2 s. The food was left in place under one randomly selected cup, and the ape could see that the food item had been left under the cup. The experimenter then continued to lift any remaining cups that had not already been lifted and continued to place his or her hand under those cups. After all cups had been lifted, the experimenter pushed forward the tray on which the cups were located. The delay between the completion of the presentation of the food and the tray being pushed forward was less than 2 s. The ape selected one of the four cups by touching it. The cup was lifted, and if the food was under it, the food was given to the ape. If the food was not hidden there, the ape made additional selections until the food was found (i.e., a correction procedure was employed). Each ape was presented with either 20 or 25 trials in this condition.

In the rotate condition, only three cups were presented, and a food item was hidden under one randomly selected cup in the same manner as in the stable location condition. The experimenter then rotated the tray on which the cups rested 180 degrees before the tray was presented to the ape. Therefore, foods hidden under the cup to an ape's left ended up in the position to the ape's right, and vice versa. Food hidden under the middle cup remained in the middle position after the 180-degree rotation. Control trials also were presented in which a second experimenter, who was unaware of the location of the hidden food, presented the tray so as to eliminate any possible cues from the first experimenter. During these control trials, the second experimenter faced away from the test apparatus during the placement of the food item, and the first experimenter faced away from the test area during presentation of the tray to the subject. Each ape was presented with 40 trials in this experiment (15 control trials and 25 trials without controls). A correction procedure was not used in this condition. If an ape made an incorrect selection, it was shown where the food was hidden but was not given the food, and the next trial was prepared.

In the shift condition, three cups again were used, and the experimenter presented the food reward in the same manner as in the previous conditions. However, after the food reward was hidden beneath one of the randomly selected cups, the experimenter changed the position of two of the three cups by moving them simultaneously and exchanging their positions on the tray. The movement occurred when the experimenter slid two of the cups across the tray. If the two cups both were located in outside positions on the tray then one of the cups slid in front of the nonmoving middle cup while the other cup slid behind the nonmoving cup. If the two cups to be moved were next to each other, one cup slid in front of the other. The hidden food always was under one of the two cups that were exchanged in position, and the final location of a given baited cup was counterbalanced for the other two positions on the tray. The experimenter then presented the tray to the ape for selection. Again, control trials were conducted in a manner identical to that of the rotate condition. Each ape was presented with 40 trials in this experiment (15 control trials and 25 trials without controls). A correction procedure was not used in this condition. An incorrect selection resulted in no food reward although the ape was shown the correct location.

The rotate and shift conditions offered two variations of spatial transpositions. In the rotate condition, all three cups moved at one time, but their proximity to each other never differed through the transposition. In the shift condition, the two cups that were moved also changed their proximity to each other (and, if they were the two outermost cups, their proximity to the middle, nonmoving cup). Therefore, the rotate condition may not be as difficult for the apes as the shift condition because of the spatial separation of the cups from each other.

Results

The performance of the apes in this experiment is presented in Table 1 and is separated by condition and by trial type (control and regular) for each ape. In the rotate and shift conditions, performance was very high for trials both with and without the control procedure described above. Therefore, the data for both control and regular trials were combined for each ape for statistical analyses. In the stable location condition, all five apes selected the correct cup on a significantly greater number of trials than would be expected by chance [all X^2 (df = 1) > 45.1; p<.01]. Four of the five apes were perfect in their performance. In the rotate condition, all five apes again selected the correct cup on a significantly greater number of trials than would be expected by chance [all X^2 (1, N = 40) > 48.3; p<.01]. Each ape was correct on the first trial. In the shift condition, all five apes selected the correct cup on a significantly greater number of trials than would be expected by chance [all X^2 (1, N = 40) > 53.0; p<.01], and each ape was correct on the first trial presentation.

Discussion

The apes were extremely efficient in retaining the spatial location of the hidden food item when that item remained in its original location during the stable location condition. On the first trial, all five apes selected the correct cup even though the food item was not visually present. Therefore, the apes did not require specific training as to the requirements of the task. As noted in the introduction, there is clear evidence that laboratory-reared apes will “spontaneously” indicate which of multiple alternatives they want to receive. The performance of the apes in this condition indicates that the apes recognized that the food item was still located under the cup that covered it.

Table 1
The apes’ performance in Experiment 1

Ape	Stable Location		Rotate		Shift	
	Control	Regular	Control	Regular	Control	Regular
Kanzi	NA	25/25	12/15	23/25	14/15	25/25
Panbanisha	NA	18/20	13/15	23/25	13/15	22/25
Lana	NA	20/20	14/15	24/25	13/15	24/25
Sherman	NA	25/25	15/15	24/25	14/15	25/25
Panzee	NA	20/20	13/15	22/25	12/15	23/25

The subsequent test conditions involved the nonvisible movement of the food items either through rotation of the entire array of cups or through movement of individual cups in that array. On the rotate trials, all five apes were efficient in gaining the food reward with their first selection despite the nonvisible movement of that food during trials. With the movement of the entire array, the apes could not rely on a fixed location as the correct reference point for selection on a given trial, but rather had to represent the movement of the food item along with the visible cup that covered it throughout the spatial transposition. On shift trials, all five apes performed once again at a very high level in monitoring the movement of the hidden food object. In this case, the location of the cup containing the hidden food item changed not only in space but also in reference to the tray itself. It should be noted that because the hidden food was always under one of the two cups that moved in this condition, the apes may have learned that the reward was only under one of those two cups. If so, this would indicate that a chance level of responding would be 50% correct rather than 33%. However, even in that case, all five apes still selected the correct cup on a significantly greater number of trials than would be expected by a chance performance level of .50 [all X^2 (1, N = 40) > 22.5; p<.01].

Therefore, the results from this experiment clearly indicate that members of the genus *Pan* can monitor spatial transpositions that occur in a relatively small area. These results contrast with those reported by Tinklepaugh (1932) for monkeys in a similar situation. The monkeys did not take into account the movement of containers (one of which contained food) but responded on the basis of the original location of the food, whereas the apes in the present experiment attended to the transpositions of the containers and tracked the container holding the food reward.

Experiment 2

The present experiment investigated whether the apes' skill in monitoring spatial transpositions transferred to a more abstract situation as could be represented on a computer monitor. These apes had considerable experience using joysticks during computerized cognitive tasks. The question was whether the apes could monitor spatial transpositions on the computer monitor as effectively as they had monitored the movement of the cups in the first experiment.

Method

Subjects. Two chimpanzees, Sherman and Lana, and one bonobo, Panbanisha, were observed in Experiment 2. The bonobo Kanzi was unavailable as a subject in Experiment 2 for reasons not related to the topic of this paper. The chimpanzee Panzee was not included in this experiment because she failed to attend to the computerized task during pilot testing, and she was uncooperative during attempted training sessions.

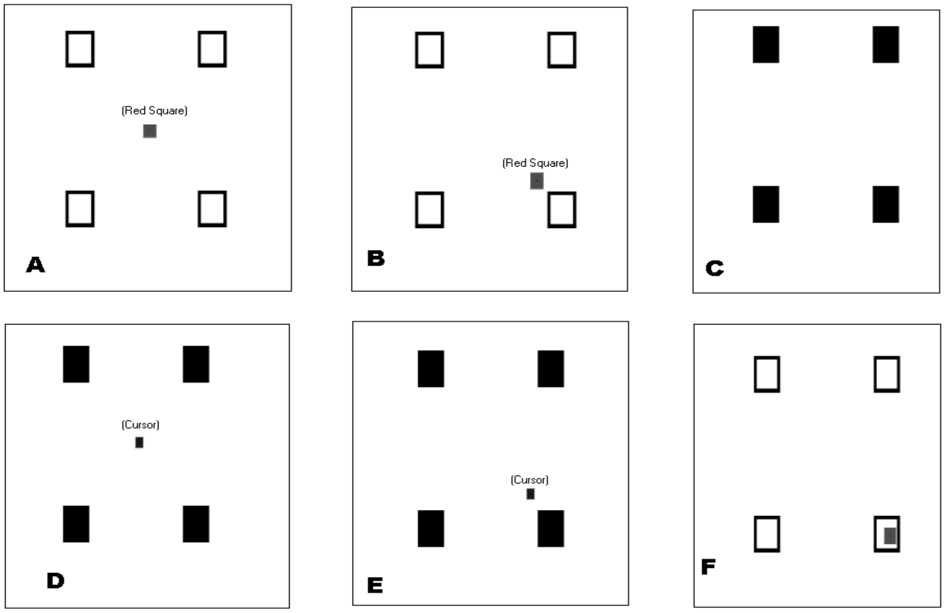

***Figure 1*.** Experiment 2, stable location condition: An ape moved a cursor on a computer monitor, using a joystick, until it came into contact with a gray start box at the center of the screen. The cursor disappeared, and four open boxes appeared in each corner of the monitor. At the same time, a red square appeared in the middle of the screen (A). The red square then moved to one of the boxes (B). Upon reaching that box, the red square "entered" the box. All four boxes then were masked with a black cover (C), and the cursor returned to the middle of the screen (D). The ape then had control over the cursor to select one of the four boxes (E). The contents of all boxed were revealed after the selection (F). The words in parentheses are provided as aids in the figure, but they were not part of the actual experimental trials.

Apparatus. Trials were presented on a Compaq DeskPro with an attached Kraft Systems joystick. The program was written in Microsoft Visual Basic for Windows.

Procedure. There were two conditions in this experiment. During the first condition (the stable location condition), at the start of each trial, subjects had to manipulate an on-screen cursor, by using a joystick, until it came into contact with a gray start stimulus at the center of the screen. Subsequently, the cursor disappeared, and four boxes appeared, one in each corner of the monitor. The term box as it is used in this paper refers to a two-dimensional square on the monitor. Each box measured approximately 5 x 5 cm. At the same time, a red square (3 x 3 cm) appeared in the middle of the screen. The red square moved to one of the boxes through five discrete movements of its position on the monitor (Figure 1). Each movement occurred after 750 ms. Upon reaching one of the boxes, the red square "entered" the box. All four boxes then were masked with a black cover, and the cursor returned to the middle of the screen. The ape then selected one of the four boxes. When a selection was made, all four boxes were "uncovered" so that the location of the red square was revealed. If the box that was selected contained the "hidden" red square, a melodic tone sounded, and the ape received a food reward from the experimenter (typically a piece of fruit). If the red square was not hidden under the selected box, a buzz tone sounded, and the next trial was initiated within a few seconds. The experimenter remained seated next to the computer apparatus during test sessions but did not view the computer monitor and was unaware of the apes' performance except as evidenced through the feedback tones for correct and incorrect trials. Daily sessions consisted of approximately 20 to 40 trials. The apes continued to work on this experimental task until they reached a criterion of 75% correct or better on their two most recent sessions. They then began the second condition.

In the second condition (the rotate condition), all four masked boxes changed locations (the spatial transposition) after the red square had moved into one of the boxes. The box in the top left position moved to the top right position, the box in the top right position moved to the bottom right position, the box in the bottom right position moved to the bottom left position, and the box in the bottom left position moved to the top left position. All four boxes moved simultaneously, and each rotation of the boxes occurred through four discrete movements on the monitor. Each of these movements occurred after 500 ms. Therefore, the perceived movement was disjointed and discontinuous. The four boxes could move to a new corner of the monitor from 1 to 4 times such that they ended up either one, two, or three corners further in a clockwise direction from their start position or back in their original position (in the case of 4 moves). When the boxes stopped moving, the cursor reappeared in the center of the screen, and the subject used the cursor to contact one of the boxes. When a selection was made, all four boxes were uncovered so that the location of the red square was revealed. If the box that was selected contained the hidden red square, a melodic tone sounded, and the ape received a food reward. If the red square was not hidden under the selected box, a buzz tone sounded, and the next trial was initiated within a few seconds. All three apes began with sessions in which there was only one rotation of the boxes during a trial. Additional rotations were added to the test sessions as an ape's performance reached a criterion of 80% correct or better for each rotation within a given session. Note that with two-rotation sessions, a given trial could involve the movement of the boxes one position further clockwise or two positions further clockwise. With three-rotation sessions, there were three possible outcomes for the hidden red square (it moved either one, two, or three positions in a clockwise direction), and with four-rotation sessions there were four possible outcomes for the hidden red square (it moved either one, two, three, or four positions in a clockwise direction). Daily sessions consisted of 20 to 50 trials.

Results

In the stable location condition, Panbanisha reached criterion in the minimum of two sessions (40 trials), and overall her performance in selecting the correct box was significantly greater than chance [X^2 (1, N = 40) = 83.3; p<.01]. Sherman reached criterion in four sessions (100 trials), and overall his performance was significantly greater than chance [X^2 (1, N = 100) = 108.0; p<.01]. Lana reached criterion in five sessions (115 trials), and overall her performance was significantly greater than chance [X^2 (1, N = 115) = 60.9; p<.01].

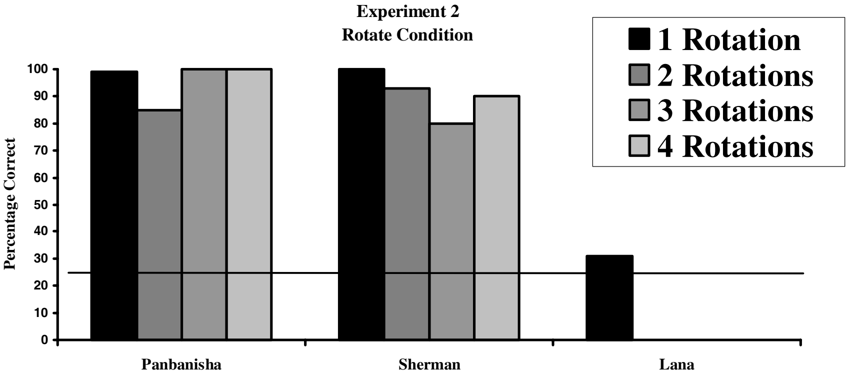

Figure 2. Results from Experiment 2, rotate condition: Each ape's performance with each rotation is presented across sessions; chance performance was 25%. For Lana, only single-rotation trials were presented.

In the rotate condition, Panbanisha required one session to reach criterion for one-rotation trials (16 trials), two sessions to reach criterion for two- rotation trials (28 trials), one session to reach criterion for three- rotation trials (11 trials), and one session to reach criterion for four-rotation trials (10 trials). Overall, Panbanisha completed 147 trials. Sherman required two sessions to reach criterion for one-rotation trials (70 trials), seven sessions to reach criterion for two-rotation trials (90 trials), eight sessions to reach criterion for three-rotation trials (89 trials), and four sessions to reach criterion for four-rotation trials (37 trials). Overall, Sherman completed 943 trials. Lana was not presented with two-, three-, or four-rotation trials because she never reached criterion with one-rotation trials even after 300 trials. The larger number of trials given to Sherman was the result of Sherman's continuing to perform trials with fewer numbers of rotations while progressing to trials with greater number of rotations. Panbanisha was so successful at the task that she did not perform nearly as many sessions as Sherman. Therefore, as sessions containing trials with greater numbers of rotations also contained trials with fewer rotations, Sherman received a larger number of these trials than Panbanisha. Although she performed fewer trials than Sherman overall, Lana never progressed beyond one-rotation trials. Sherman only needed 70 trials with one rotation before moving on to sessions with one- and two-rotation trials. Therefore, he was performing much better (>90%) on one-rotation trials than Lana within the first 100 exposures to them.

The overall performance of each of the apes in the rotate condition is presented in Figure 2. For the single session on which Panbanisha met criterion with all four rotations, her overall performance was significantly better than chance [X^2 (1, N = 40) = 104.5; $p<.01$]. For the single session on which Sherman met criterion with all four rotations, his overall performance also was significantly better than chance [X^2 (1, N = 40) = 112.1; $p<.01$].

Discussion

All three apes had some previous experience working on computerized tasks in which stimuli on the screen were masked or removed during a trial (as in the delayed matching-to-sample procedure), and the apes had to continue to represent those stimuli in some way. The results of the rotate condition in the current experiment indicated that two of the three apes monitored the spatial transposition of objects on a computer screen by attending to the location at which the red square was hidden and by tracking the movement of the masking agent (note, however, that the fourth animal could not be tested using this apparatus and, thus, the overall success rate for this sample of apes was 50%). These apes attended to the movement of the correct box (i.e., the one that covered the red square) despite the simultaneous movement of the remaining three boxes. This was true for varying distances as the boxes could move for either relatively short distances (one move) or relatively long distances (four moves). Additionally, the movement on the monitor was very complex. The discontinuous nature of the perceived movement was novel for the apes, and the movement required complex visual coordination of information regarding the location of the relevant box.

One of the chimpanzees was not very successful during the rotation trials despite performing well on the stable location trials. Lana's errors were not consistent in any way, and her incorrect selections were made equally often for each location. Lana's difficulty appeared to stem from her failing to view the monitor after the red square was hidden. She often looked around the test area while waiting for the cursor to reappear, and thus failed to monitor the movement of the boxes on the screen.

During these trials, although the apes sometimes removed their hands from the joystick while the array of boxes was rotating, they left their hands on the joystick for the majority of the trials. Although the experimenters observed no clear motor responses with the joystick during the time when the cursor was not visible and the array of boxes was moving, finer measures of motor responding during the rotations were not recorded during the experiment. It would be interesting to note whether any motor movement occurred that might have acted as a cue for the animals (i.e., perhaps the apes were tracking the movement of the relevant box by slightly moving the joystick in the same direction). Additionally, it would be useful to track the apes' eye movements during the rotation of the boxes to determine whether the discrete movements of the boxes were followed continuously or whether the apes were waiting until the entire array had finished moving before re-establishing eye contact with the relevant box. This would allow an analysis of whether the apes continuously tracked the target box throughout a trial or attended only to the number of rotations and responded according to that number. It is possible that the apes learned the contingencies between the start location of the red square and the final box to be selected on the basis of number of rotations executed. However, this is highly unlikely for at least one of the apes (Panbanisha) due to the high performance level exhibited from the earliest trials. Panbanisha was correct on the very first trial with one rotation, three rotations, and four rotations (and, in fact, never made an error in three- or four-rotation trials and made only one error in single rotation trials). Therefore, she did not require multiple trials to learn these contingencies.

General Discussion

The apes' performance on these two experiments indicates that both bonobos and chimpanzees monitor spatial transpositions. Additionally, these experiments demonstrated that the medium through which spatial transpositions are presented affect performance in apes to some degree. However, the more abstract spatial transposition (the computerized task) was monitored by two of the four apes in Experiment 2. Unlike in the real world experiments, the computerized tasks did require some amount of training to teach the apes that the requirement of the task was to select the box containing the red square. Additionally, whether the apes interpreted the computerized task as one in which the red square was a cue as to which box to monitor (an interpretation not requiring object permanence) or whether the apes interpreted the task as one in which the red square was to be "found" (similar to finding the hidden food in Experiment 1 through recognizing object permanence) is not clear.

In Experiment 1, the apes' performance demonstrates that members of the genus *Pan* perform at least as well as human children aged 3.5 to 4 years old (Sophian, 1986). Monitoring spatial transpositions on a computer monitor is a more abstract form of spatial cognition than monitoring the movement of cups, other apes, or predators. However, two of these apes were able to monitor such abstract spatial movements. The computer tasks dissociated the food reward from the behavior of monitoring the movement of an object in that the apes were not tracking the item that they wanted (the food reward). In addition, the movement of the boxes on the screen occurred in discrete stages, not in a more natural and fluid way. This movement is arguably more difficult to monitor, thus making the task more difficult than in the first experiment. Additionally, four boxes moved at the same time, and this was a greater number than in the experiments with the cups. To the authors' knowledge, no similar computerized tasks have been presented to other nonhuman primates. Therefore, this is the first experimental evidence that nonhuman primates monitor spatial transpositions in a simulated computer task.

We note the special nature of the apes included in this experiment: All five had some degree of language-training and were exposed to language-enriched rearing environments (Rumbaugh, 1977; Savage-Rumbaugh, 1986; Savage-Rumbaugh & Lewin, 1994). For this reason, we believe it will be necessary to compare the results from these apes with those of nonlanguage-competent apes as well as with other nonhuman primate species to determine whether this special rearing affects spatial monitoring.

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