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Can Monkeys (*Macaca mulatta*) Represent Invisible Displacement?

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Four experiments were conducted to assess whether or not rhesus macaques (*Macaca mulatta*) could represent the unperceived movements of a stimulus. Subjects were tested on 2 computerized tasks, HOLE (monkeys) and LASER (humans and monkeys), in which subjects needed to chase or shoot at, respectively, a moving target that either remained visible or became invisible for a portion of its path of movement. Response patterns were analyzed and compared between target-visible and target-invisible conditions. Results of Experiments 1, 2, and 3 demonstrated that the monkeys are capable of extrapolating movement. That this extrapolation involved internal representation of the target's invisible movement was suggested but not confirmed. Experiment 4, however, demonstrated that the monkeys are capable of representing the invisible displacements of a stimulus.

The ability of nonhuman primates to represent internally the unperceived movements of a stimulus object has been the focus of object permanence research for years (see Natale & Antinucci, 1989, and Dore & Dumas, 1987, for reviews). Invisible displacement tasks, used to assess the representational capacity of a subject, are notoriously difficult for monkeys to solve nonassociatively. In an invisible displacement task, the subject is shown a food object that is placed into an opaque container. This container is then moved behind a screen or under a block where the food object is transferred from the container to behind the screen or under the block without the subject's being able directly to perceive this transfer. The container is then moved out from behind the screen, and shown empty to the subject. After seeing the container empty, if the subject searches behind the screen or the appropriate screen if there is more than one, rather than search around the now empty container, it is presumed that the subject is able to represent internally the invisible displacement of the food object from the container to behind the screen. However, subjects often can solve this task associatively, so there are usually a variety of control procedures used as well. Currently, there are no consensual reports of monkeys being able to solve this task by using a representational process. Thus, it has been concluded that monkeys lack the representational capacity to infer the movements of an unperceived object (Dumas, 1992; Natale & Antinucci, 1989).

Movement representation has not been a widely researched phenomenon in nonhuman primates. Very little is known about how nonhuman primates perceive and respond to the unseen movements of objects as might occur in a variety of contexts. There is some evidence to suggest that baboons are capable of representing internally the unperceived rotations of a stimulus. Using a mental rotation paradigm, Vauclair, Fagot, and Hopkins (1993) found that the decision time for baboons to make a correct comparison between a sample stimulus and a rotated version of it increased linearly with an increase in the angular disparity between the two stimuli, which is the same pattern found in humans (though it seems to be lateralized in baboons). The sample stimulus itself does not rotate (and hence is not directly perceived) but rather is "imagined" by the subject. The analogical response pattern demonstrated by the baboons suggests that they, like humans, can represent internally the unperceived rotations of a stimulus.

Representing the unperceived rotations of a stimulus has been investigated in one nonprimate species. When a testing paradigm was used in which pigeons observed a clock hand stimulus move at a constant rate, disappear, and then reappear at a subsequent location, Neiworth and Rilling (1987) found that, after training on specific degrees of stimulus rotation, pigeons could correctly identify violations of clock hand movement on novel trials (a violation would occur if the hand reappeared at an inappropriate location given its constant speed of movement as indicated by the delay between stimulus disappearance and reappearance). That is, the pigeons could discriminate between appropriate and inappropriate locations of clock hand reappearance when

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the hand reappeared at novel degrees of rotation from its initial, visible location. Neiworth and Rilling interpreted these results as evidence for the use of imagery by pigeons. If the pigeons were responding on the basis of "imagining" the unseen movements of the clock hand stimulus, it would suggest that they were representing internally the unperceived rotations of the stimulus.

Though the tasks used in object permanence and mental rotation paradigms are quite different in procedure and likely in demand, they are designed to examine a subject's ability to represent internally stimulus movement that has not been directly perceived. It is important to clarify that the ability to represent internally the unperceived portions of stimulus movement is the ability to represent invisible displacement. *Displacement* means movement (be it a discrete event as in invisible displacement tasks or a relatively continuous event as in mental rotation), and if the movement is made to be invisible in one way or another, then empirically, not necessarily subjectively, invisible displacement (or displacement transformation as is involved in mental rotation; Gallistel, 1990) has occurred.

In the current series of experiments, the ability of rhesus monkeys (*Macaca mulatta*) to represent invisible displacement was examined through a target prediction paradigm, which involves the use of a computerized testing system (CTS). In target prediction tasks, subjects contact a moving target with a joystick-controlled cursor. Contact can be made by either chasing and catching a target or by shooting at the target from a stationary turret. Washburn and colleagues (Washburn, 1992a; Washburn & Rumbaugh, 1992) have demonstrated that rhesus monkeys, like humans, respond predictively to a moving target. Whether subjects are chasing moving targets (CHASE) or firing shots at a moving target (LASER), they use paths of movement or shot angles that approximate significantly the hypothetically optimal path (or shot angle) that would be used if one were predicting the movement of the target. Moreover, for the LASER task, the monkeys (like humans) are able to determine whether or not a shot will intersect with the moving target, and they can abort errant shots (shots that would have missed the target) before they have traversed even half the distance to the target.

The predictive quality of the monkeys' responses on target prediction tasks provided us with an opportunity to test their performance when the target undergoes invisible displacement. Unlike these previous tasks, the tasks used in the current set of experiments involved predicting target movement when a portion of its path became occluded. In the HOLE task, we created an apparent (two-dimensional) occluder by generating from the computer a visibly outlined region on the monitor in which target movement became invisible. In the LASER task we made the occluder more real by placing an opaque card on a quadrant of the monitor, blocking visibility of a portion of target movement. The use of an occluder, be it apparent or real, allowed us to examine the ability of rhesus macaques to represent internally the invisible displacements of target movement.

Experiment 1

Method

Subjects. Two rhesus monkeys (*Macaca mulatta;* Abel and Baker; Charles River Laboratories, Wilmington, MA) were tested in this experiment. At the time of this experiment, these male monkeys were 9 years of age and had been trained to manipulate a joystick to respond to a variety of computer-generated tasks (Rumbaugh, Richardson, Washburn, Savage-Rumbaugh, & Hopkins, 1989; Washburn & Rumbaugh, 1994). Each monkey was tested unrestrained within its home cage and was not deprived of food or water for purposes of testing.

Apparatus. The monkeys were trained and tested with the Language Research Center's Computerized Test System (LRC-CTS), which consists of a battery of software tasks and the computer hardware required to administer them (see Rumbaugh et al., 1989). Each of the LRC-CTS test stations consisted of a computer monitor and a standard analog joystick, both connected to a 386sx computer. The subjects were required on each trial to manipulate the joystick to direct a computer-generated cursor (a 1.25 cm × 1.25 cm white plus sign, +) into contact with two-dimensional, multicolored stimuli generated by the computer and randomly presented on the monitor. Sound feedback was provided via an external speaker–amplifier located on top of the monitor. A 97-mg fruit-flavored chow pellet (P. J. Noyes, Lancaster, NH) was automatically dispensed to reinforce trials that were completed correctly.

Task. In this task (called HOLE), the subject had to manipulate the joystick so as to bring the cursor into contact with a 1.25 cm × 1.25 cm blue square (the target). Each trial began with the presentation of a circle in the center of a black computer screen. The circle was outlined in white and 15 cm in diameter. The cursor and the target were also presented on the screen, each in random position (but neither within the confines of the circle). The target stimulus moved continuously on the screen in a diagonal pattern, "bouncing" off the screen boundaries at 45° angles. The target moved at a speed of approximately 3 cm/s when it was outside of the large circle; inside the circle, the target changed in appearance (see below) and traveled at approximately 1 cm/s. The slower target speed within the circle allowed enough time for subjects to move the cursor around the region before the target reappeared. The cursor could not enter the large circle. Thus, the circle presented a semipermeable barrier through which the target could travel (albeit slowly) but around which the cursor had to move. The task was designed to reveal whether the monkeys would learn to circumnavigate the large circle so as to catch the target at the point where it exited the barrier.

Auditory feedback and pellets were provided whenever the subject "caught" the moving target, regardless of whether or not the target had moved through the circle. For each trial, the computer recorded response time (the time from first joystick movement until collision between the cursor and target) as well as the x–y coordinates of every cursor and target movement made during the trial.

Procedure. The HOLE task was administered under two conditions. On some trials (visible condition), the target changed into a 0.75 cm × 0.75 cm white box whenever it was inside the large circle. On other trials (invisible condition), the target was not visible against the black background of the screen while it was inside the large circle. In all other ways (speeds, direction of movement, etc.) the two conditions were identical. Thus, in the former condition the subjects could move the cursor to a point where the visible target would emerge from the circle, but in the latter condition the subjects were required to determine an appropriate point of intersection with the invisible target on the basis of its trajectory when it disappeared into the circle.

Both animals were initially trained only in the visible-target condition. Before this experiment, each monkey had performed many thousands of trials on computer tasks requiring them to catch moving targets (albeit none with semipermeable obstacles); as a consequence, they learned quickly to catch the moving target. Subsequently, each animal performed an additional 2,000 trials, in 10 blocks of 200 trials. Trial condition (visible vs. invisible) was alternated across trials in this condition.

Results

In both conditions, the monkeys were frequently able to catch the target before it entered the circle even once. These trials were omitted from subsequent analysis. On the remaining trials, the distance in degrees between the cursor and the target was computed each time that the target exited the circle. These distances were averaged across blocks of 200 trials for each monkey. No evidence of trend was observed across blocks of trials for either monkey in either condition; that is, neither monkey generally improved in performance with practice. Given this, the data were grouped by animal and analyzed as a function of visible versus invisible target condition.

A significant main effect was observed for target condition, $F(1, 18) = 109.04$, $p < .01$. The monkeys were significantly closer to the target as it exited the circle in the visible condition than when the target was invisible (58° and 98°, respectively). In fact, on almost all of the invisible trials the monkeys chased the target until it disappeared into the circle, whereupon the animals stopped manipulating the joystick and permitted the cursor to remain in position until the target reappeared as it emerged from the circle. In contrast, the monkeys generally approximated the target's point of exit from the circle when the target was visible (comparing the average distance observed for this condition with the distance expected by chance alone; 90°). Abel was significantly better at moving to the point of exit from the circle than was Baker, $F(1, 18) = 28.41$, $p < .01$ ($M = 67°$ vs. 89°, respectively); however, this effect did not interact with trial condition ($p > .05$), indicating that the pattern of results was comparable for the two monkeys.

Discussion

These results provide no evidence that the monkeys can respond to targets that disappear on the screen. In contrast, the data suggest that the monkeys had no idea what to do when the target disappeared, despite being fully capable of circumnavigating the circle to capture visibly moving targets. Perhaps the monkeys lacked the ability to generate and represent internally the continued path of the invisible target based on the trajectory of movement that characterized its entry into the circle.

Alternatively, this suggestion contradicts the findings of Washburn (1992b) that these same rhesus monkeys could estimate the invisible continuation of a "shot" and determine accurately whether the shot would hit or miss a computer graphics target. The tendency for the monkeys to do nothing while the target was invisible (rather than to move the cursor to a point that does not correspond to the appropriate target trajectory) suggests an alternate interpretation. Before the present experiment, the only experience the animals had with target stimuli that became invisible was with memory tasks such as delayed matching to sample and sameness–difference (e.g., Washburn and Rumbaugh, 1991a). Once the cursor is brought into contact with the target stimuli in these memory tasks, the targets disappear for a retention interval of various lengths. During the retention interval, the cursor remains on the screen but does not move with manipulations of the joystick. Only after the retention interval, when stimuli are again presented on the screen, can the subject respond. Given the pattern of present results, including the description of each monkey's behavior in the invisible target condition, it seems possible that the monkeys interpreted the disappearance of the target into the circle as a type of retention interval, during which responding was fruitless. The next experiment was designed to assess this possibility.

Experiment 2

Method

The subjects, apparatus, and procedure for this experiment were identical to those of Experiment 1, with the exception of one change to the HOLE task. In the previous experiment, the target moved continuously in a diagonal pattern around the screen whether or not the cursor was moving. In almost all other tasks that the monkeys had experienced, target movement was contingent on cursor movement, such that all was stationary on the screen unless the joystick was being manipulated (see Rumbaugh et al., 1989). For Experiment 2, target movement was made contingent on cursor movement. At any time that the cursor stopped, the target also stopped, whether or not it was in the circle. Note that this procedure required subjects to manipulate the joystick and thus move the cursor continually so as to draw the target out of the circle. Any trial in which the subject moved the cursor and then released the joystick (so that neither the cursor nor the target moved) for 60 consecutive seconds was aborted and a new trial was initiated.

Each subject performed 2,000 trials under these parameters in the visible target condition. Subsequently, each monkey performed 2,000 trials in which target condition (visible and invisible) was alternated across trials. As in Experiment 1, trials were discarded in which the target was caught before it entered the circle at least once.

Results

Each monkey rapidly learned the task under the new parameters. More important, the monkeys immediately generalized to the invisible target trials, moving the cursor around so as to keep the invisible target moving through the circle until it reappeared and was caught. Only 8% of the trials in the invisible condition were aborted because the monkeys stopped moving the joystick, a number that was not different from the percentage observed for the visible condition (5%; $p > .05$).

In the analysis of average distance data, both monkeys exhibited slight but reliable improvement across blocks of trials in the invisible condition (improving from an average distance of 32° away from target's exit site in the first blocks to 21° in the terminal blocks of trials $r_{\text{autocorrelation}} = .49$, $p < .05$). Consequently, analysis of variance was deemed inappropriate for the present analysis; however, the subjects were reliably closer to the target in the visible than the invisible condition (Wilcoxon signed rank test, $p < .01$). Although the mean distance from the cursor to the target in the invisible condition (36°) was larger than when the target remained visible (20°), performance in both conditions was substantially better than in Experiment 1. Unlike in the prior experiment, subjects were consistently closer to the target's point of exit than the difference expected by chance (90°) even when the target disappeared while inside the circle (Wilcoxon signed rank test, $p < .05$). These differences are illustrated in Figure 1.

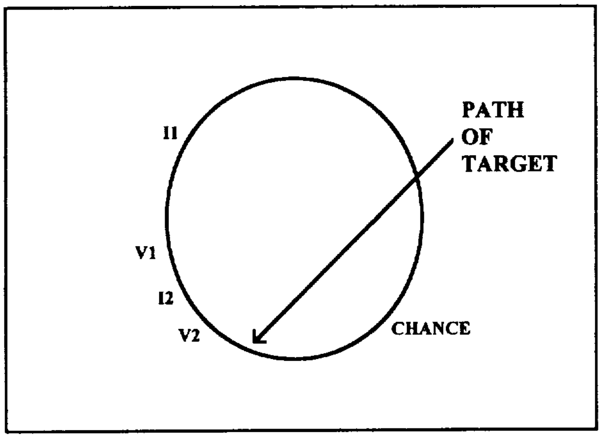

Figure 1. The average distance between the cursor and the exit point of a target (given an illustrative target trajectory) in Experiment 1 visible (V1) and invisible (I1) conditions, compared with Experiment 2 visible (V2) and invisible (I2) conditions. Chance-chance accuracy.

Discussion

The monkeys were able to estimate, with high levels of accuracy, the place where an invisible target would emerge from the circle based on the trajectory of movement that characterized the target's entry into the circle. It is noteworthy that performance in both conditions was improved when target movement was made contingent on cursor movement. This was the case despite the fact that the subjects were required to move the cursor back and forth around the exit site to keep the target moving through the circle. That is, even if the monkeys could generate an accurate exit site from the trajectory of target entry, they could not simply move to that location and wait for the target to reappear. The cursor had to be moved in order to produce movement of the target (even when it was invisible), and this movement undoubtedly inflated the error for these measures. Nevertheless, improvement over Experiment 1 performance was most dramatic for the invisible target condition, where performance came to approximate levels of accuracy typical for the visible target condition. This suggests that the monkeys could extrapolate the movement of the invisible target, perhaps even by representing its intermediate positions across the circle. Additional evidence that the monkeys were responding on the basis of inferred movement of the invisible target is provided by the fact that the monkeys did continue to move the joystick when the target disappeared into the circle so as to keep the target moving through the circle.

Of course, each monkey had performed thousands of HOLE trials by the time these experiments were complete.[1] Thus, it might be argued that the animals had simply learned a series of entry–exit associations that they could use to capture the target efficiently without extrapolating and representing internally the movements of the invisible target. We designed Experiment 3 to test this suggestion. Novel target-movement paths were introduced to determine whether the monkeys were responding on the basis of entry trajectory or more simple associations. If the monkeys were responding using spatial associations, they should respond to these probe trials by moving to an exit point previously associated with the particular point of entry. Alternatively, individuals capable of representing the invisible displacements of the target should be relatively unaffected by the particular trajectory presented on any given trial.

Experiment 3

Method

The monkeys, apparatus, and procedures used in this experiment were identical to those in Experiment 2, except for a single change to the HOLE task. On each invisible target trial, the target moved at a randomly selected angle relative to horizon (25°, 45°, or 65°) across the screen and through the circle. As in previous experiments, the target moved at a 45° angle on all trials in which the target remained visible.

Each monkey performed 200 trials of the HOLE task with these parameters, alternating on each trial between the visible and invisible conditions. Given the number of potential entry–exit sites, each of the trials in which a movement angle other than 45° was used represents a novel transfer test for this experiment.

For comparison, 10 human volunteers were also tested in this experiment. Each of these undergraduate students (6 women and 4 men, ages 18–34 years, who participated in exchange for class credit) performed 48 trials of the HOLE task in which the target

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[1] In fact, the experiments reported here were conducted over a span of several years, during which time the monkeys performed many thousands of trials of HOLE and other tasks. Between Experiment 1 and Experiment 2, for example, thousands of HOLE trials were performed; however, no improvements in HOLE performance were observed until the conditions of Experiment 2 were introduced.

moved at 45° angles and remained visible or became invisible on alternate trials. In a second block of 48 trials, the target moved either at a 25°, 45°, or a 65° angle, which was randomized each trial. Again, whether or not the target remained visible while in the circle was alternated across trials. The initial position and direction of movement for the target was randomized each trial.

Results

The average distance between the cursor and the invisible target's exit point when it emerged from the circle, as a function of species and movement angle, is shown in Table 1. Human participants missed the exit point of a visible target by an average of only 14°. For the monkeys, the average distance on the visible target trials was comparable to those reported in the previous experiments (22°). Performance in the probe conditions (invisible target, 25° or 65° movement) was comparable for both species to performance on the 45° trials. The observed distances were much less than the 20° difference in error that would be expected if the subjects moved on the basis of simple stimulus-response associations to a point 45° across the circle from each point of target entry.

Discussion

Taken together, these experiments suggest that the monkeys can respond appropriately to stimuli that become invisible, and that they do so by using a generalizable process such as the extrapolation of movement. These findings cannot be attributed to low-level associations between stimulus and response conditions.

However, the ability to determine the point of exit from a barrier does not necessarily require the internal representation of each target movement within the barrier. In fact, it is not certain that the monkeys perceived the circle as an occluder—that is, as an area behind which or within which the target can be invisible—at all.

We conducted Experiment 4 to provide clearer evidence of subjects' ability to represent the intermediate points of invisible stimulus movement. A new task (LASER) was used that did not require subjects to wait for the target to reappear in order to contact it. Shots could be fired at the target while it was moving behind the occluder. By creating a real rather than an apparent occluder, we could determine more definitively whether or not subjects were capable of representing the invisible displacements of a moving target.

Table 1
Error Estimating Exit Point of Invisible Targets as a Function of Target Movement, Angle, and Species

	Target angle		
Species	25°	45°	65°
Human	26°	24°	29°
Monkey	27°	30°	36°

Experiment 4

In the previous experiments, the circle provided a "virtual occluder" that hid portions of target movement. However, the impenetrability of the circle to the cursor limited the flexibility of responding, obscuring whether or not subjects understood that the target was moving invisibly through the hole and were responding on the basis of that knowledge. For the present study, the LASER task was administered either with or without a real mask—a piece of black cardboard attached to part of the screen, creating a region that occluded target movement. Importantly, the target moved from left to right or vice versa in a zigzag pattern, and it began in a randomly selected location for each trial. Hence, the target's movement, though at predictable 45° angles, differed on each trial as a function of its initial location and direction of heading for each trial. Because of its zigzag motion, the target frequently changed directions, like a deflection. These deflections are important because they would go unperceived when the target was occluded.

If subjects failed to recognize the cardboard as an occluder (that is, they did not recognize that the target existed and was moving behind the mask), it was expected that they would either fire shots in random directions or not respond at all until the target reappeared. However, if the monkeys realized that the target both existed and continued to move behind the cardboard, they should have directed shots toward where the target was going (i.e., at a point of intersection ahead of the moving target), even if this point itself was not visible.

Method

Subjects. The same two monkeys used in the HOLE experiments were tested in this experiment. Subjects were 11 years old at the time of this experiment. Six human volunteers were also tested. The undergraduate students (2 women and 4 men, ages 21 to 30 years) participated in exchange for course credit.

Apparatus. The same apparatus as that used in the previous experiments was used for this study. In Experiment 4, however, all subjects were tested on the LASER task (which permits responses to be made while the target is behind an occluder, rather than encouraging the animals to position a cursor at the point where a target will exit the occluder as in the HOLE task). The LASER task has been described in detail elsewhere (Washburn, 1992b). For the LASER task, subjects needed to shoot at a target moving across the monitor. The target was a blue square (3 cm × 2 cm), which moved at a speed of 4 cm/s across the top 7.5 cm of the monitor in a zigzag (or sawtooth) pattern. A shot could be fired from a stationary turret located at the middle bottom of the monitor (see Figure 2). Shots were fired at an angle corresponding to the direction of joystick deflection and could be aborted by moving the joystick handle in a downward direction. One trial consisted of the target's moving back and forth until the subject successfully hit the target. Hence, each trial may have consisted of several completed but errant shots, several aborted shots, and one accurate shot. When the target was hit, a reward tone occurred, one pellet was dispensed, and the screen was cleared for a 5-s intertrial interval. The initial target position and movement direction was randomly selected each trial.

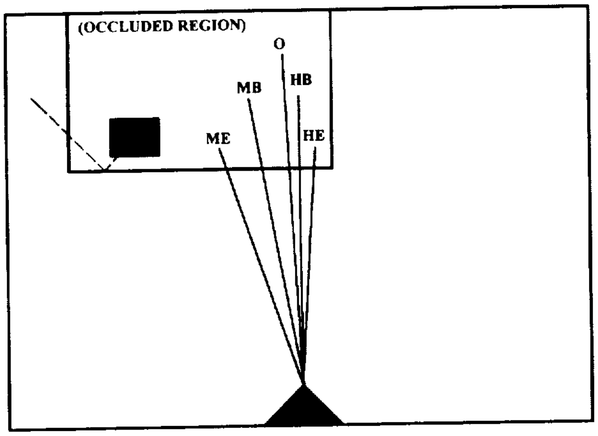

Figure 2. Depiction of the appearance of the screen in Experiment 4. Note that the mask region was covered by cardboard in the experimental condition. In addition, optimal and average shots, given the target position and path of movement, are reported for monkeys in the baseline (MB) and experimental (ME) conditions, for humans in the baseline (HB) and expeimental (HE) conditions.

Procedure. The rhesus monkeys initially performed 100 trials on this version of the LASER task to establish baseline performance. Subjects were then tested for another 100 trials on the same task but with one rectangular piece of cardboard attached to the upper left quadrant of the monitor for 1 subject and to the upper right quadrant for the other subject. This cardboard mask was covered with black electrical tape (to prevent light from passing through) and measured 7.5 cm high × 12.5 cm wide. It was attached with tape to the surface of the monitor such that it occluded a portion of the viewing surface (see Figure 2). The edge of the cardboard mask was positioned approximately 3 cm from the side of the monitor, so that the target was visible on both sides of the cardboard and no image of the target could be seen through the mask.

For each trial, the pixel-by-pixel coordinates for every shot and target movement were recorded on the computer. These data were analyzed to determine (a) the angle at which a shot was fired; (b) whether or not the target was in the region of the cardboard mask (which would have been in place to occlude the target only in the experimental condition) when the shot was initiated; (c) whether the shot was aborted, was a miss, or a hit; and (d) whether the shot was fired ahead or behind the moving target. The angle of each shot that was initiated while the target was behind the mask (or in the corresponding position for baseline trials) was also compared with the angle that would have characterized the shot if it had been fired directly at the target, and to the optimal angle for intersection. The optimal angle was determined by the target's empirical location (be it visible or occluded), heading, and speed of movement. This comparison of angles was used in a correlational analysis, described in detail elsewhere (Washburn, 1992a; Washburn & Rumbaugh, 1992).

Each human participant completed 50 trials of the LASER task in the baseline condition (no mask) and 50 trials[2] in the experimental condition (with the cardboard mask). The order in which these two conditions were administered was counterbalanced across participants.

Results

We used a difference of proportions (two-tailed z) test to analyze the averaged human and monkey data. Humans and monkeys performed similarly with respect to the average number of shots required to hit the target when it was visible or invisible (human: 2.89 and 3.74 shots/trial, respectively; monkeys: 2.66 and 3.47 shots/trial, respectively). More important, however, humans and monkeys did not differ significantly in either their hit rates for each version of the task or in the degree to which hit rates were disrupted by the presence of the occluder. The hit rate is based on only those shots that were initiated while the target was occluded or in the corresponding, but visible, region of the monitor in the baseline version. On average, 25% of the monkeys' shots and 27% of the humans' shots were hits when the target was occluded ($z = -5.55, p > .05$). When the target was visible, 48% of the monkeys' shots and 36% of the humans' shots were hits ($p > .05$).

That only one fourth of subjects' shots were hits reflects how difficult the occluded version of the task was. Even when the moving target was visible, achieving an interception was not so easy for either monkeys or humans. It is also noteworthy that when the target was occluded, neither the humans nor the monkeys ever aborted a shot that would have hit the target. Both groups accurately aborted shots that would have missed.

This similarity in monkey and human performance is further elucidated in the analysis of shot-path patterns (for complete shots initiated while the target was in the mask region). For monkeys responding in the visible target condition, the angle at which a shot was fired correlated significantly with both the location of the target ($r = .60$; $r_{\text{crit}} = .26, p < .01$) and the angle for optimal intersection with the moving target ($r = .65$). The angle of shots taken by humans was also significantly correlated with the location of the visible target ($r = .57$) and the angle of optimal intersection with the target ($r = .71$). Thus, subjects tended to fire ahead of the moving target, at an angle that generally but imperfectly approximated the hypothetical angle of optimal intersection (which was itself highly correlated with target position in this study, $r = .88$). Figure 2 depicts this pattern, with a typical baseline condition shot generated from the multiple regression formula provided by this analysis, and with comparable data from human participants.

In the experimental condition, the angle at which the monkeys shot remained significantly correlated with target location ($r = .45$) and optimal path ($r = .42$). Thus, the monkeys continued to anticipate the movement of the occluded target, albeit with less accuracy (i.e., more noise) in approximating the optimal path for a shot. Again, these results compare favorably with findings from human participants (visible condition: $r = .39$ and .46, respectively),

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[2] This number of trials was selected to maximize the number of responses obtained without boring or fatiguing the students. Performance on this relatively simple task did not change across trials, suggesting no need for additional training or testing of human participants.

as is illustrated in Figure 2, with a shot generated for the experimental condition using the regression coefficients obtained in the analysis.

Discussion

Three basic findings emerged from Experiment 4: (a) The subjects continued to respond to target stimuli, even when the target disappeared behind the occluder; (b) these responses were not haphazard but were similar to shots fired at targets that were visible; and (c) performance by the monkeys was qualitatively comparable to that of humans, whether or not the target was visible. These results indicate that the monkeys, like the humans, were capable of extrapolating the trajectory of an occluded target by using a less-than-perfect internal representation of its intermediate points of movement. Because the hit rate was based on only those shots that were initiated while the target was still behind the occluder, we have ruled out the possibility that subjects were simply lying in wait and firing shots only after the target had reappeared.

Moreover, as indicated by the correlational data, the subjects did not simply fire "blindly" ahead of the occluded target; rather, their shots tended to be accurate approximations of the appropriate shot given the inferred position, direction, and speed of the target's movement. For any given shot fired while the target was occluded, its angle was compared with the optimal angle. Shooting ahead of the target without regard for location, heading, and speed of movement behind the occluder would not likely result in shot angles that correlate significantly with an angle (the optimal one) that is empirically determined by these same factors.

It is noteworthy that all participants, regardless of species, fired at targets even on the first trials in which the targets passed behind the occluder. Thus, although training and experience clearly impact performance (e.g., learning that a target moves predictably, improving the psychomotor skills required for accurate responding), knowledge that an occluded target could nonetheless be shot did not require special training or reinforced history. Humans and monkeys alike responded accurately, that is, as if the cardboard mask merely obscured a portion of otherwise normal target movement.

The general shot angle used by subjects, as depicted in Figure 2, indicates that when the target cannot be seen, humans do tend to overshoot the point of intersection, whereas monkeys tend to undershoot the point of intersection. This result may be due to differences in representing the speed of target movement (see below).

Together, these results suggest that the monkeys were able to represent, though imperfectly, the intermediate target position or positions between the entry and exit points of the mask. That is, monkeys like humans knew that the target was still moving on the screen and that it could be shot even when it was not visible. The subjects' performance on the experimental condition of the LASER task indicates that rhesus monkeys are capable of representing the invisible displacement of an unperceived stimulus, albeit less accurately than when more perceptual information is available to them (as was the case for human performance as well).

General Discussion

In this series of experiments, we have demonstrated that rhesus monkeys are capable of extrapolating movement. The results of Experiments 2 and 3 suggest, but do not confirm, that this extrapolation involves the use of an internal representation of the target's invisible movements. Interestingly, subjects generalized this extrapolative process from familiar to novel probe trials in the HOLE task. Subjects' less-than-perfect estimates of the target's exit point in the invisible condition of the HOLE task was likely due to the requirement of keeping the cursor moving in order to have the target emerge or reappear from the occluded region. That subjects' estimates were skewed even when the target's movement through the hole was visible supports this interpretation.

Although the monkeys had extensive training on the HOLE task, it is untenable to suggest that their performance in Experiment 3 was based on the use of an associative process. Subjects' novel probe performance would have been at levels equal to or even less than chance (due to overlearning) if this had been the case. Similarly, performance on even the first trials of Experiment 4 belies the interpretation that the subjects required specific stimulus-response reinforcement experience in order to solve the novel problems introduced by an occluder.

In contrast, the monkeys' performance in the experimental condition of the LASER task demonstrates that they are capable of representing and, hence, inferring invisible displacement. It is interesting to note that both the monkeys' and the humans' performance demonstrates that representing internally the invisible displacements of a target moving in a zigzag pattern is not an easy task, nor one that is perfectly accomplished. Although subjects missed the target frequently, they were clearly using shot angles that reflected a relatively accurate estimation of where the target was located and heading behind the occluder, as is evident in the significant correlation between their shot angles and the optimal shot angle. Subjects' average hit rate of about 25% in the occluded condition could be taken to reflect a less than perfect representation of the target's speed or zigzag motion. It would not be surprising if subjects were misrepresenting speed to some extent. Finke and his colleagues (Finke, Freyd, & Shyi, 1986; Freyd & Finke, 1984) have conducted several studies demonstrating that humans overestimate the movements of an object in their representations. This phenomenon of representational momentum supports our findings for the humans (as seen in Figure 2) and may offer some insights into the nature of the monkeys' representations of movement as well.

Tracking and Extrapolation Studies

The similarity of HOLE and LASER to extrapolation tasks (Etienne, 1984; Krushinsky, 1990) and infant visual tracking tasks (see Bremner, 1985, and Harris, 1987, for reviews) is evident, but there are some significant differences. In none of these previous tasks is the subject ever required to give an estimate of target reappearance that is any more precise than simply "the other side of the occluder," nor is the object's path of movement anything other than linear and, generally, familiar (but see Nelson, 1971). The use of such procedures makes for conditions that are highly conducive to associative or local learning.

The HOLE task allows subjects to produce a relatively precise estimate of where on the other side of the occluder targets with novel entry point trajectories will reappear. Because the occluder is a circle, there are more degrees of freedom involved in determining the location of target reappearance. It is not simply an expectation of target reappearance or event prediction (Bremner, 1985; Goldberg, 1976) that is being tested but an estimation of a specific exit point location, out of a range of possible exit points, given a novel entry point trajectory. For the LASER task, the pattern of target movement is a zigzag, often involving unseen deflections, and subjects are allowed to (and did) respond to the target while it remained occluded. Subjects fired shots ahead of as well as into the occluder, suggesting that they were not simply firing at some anticipated location of target reappearance but at where they estimated the target's location and heading behind the occluder would be. These features of the HOLE and LASER tasks offer a more sensitive evaluation of subjects' ability to extrapolate and represent unseen movement.

Object Permanence

Having demonstrated that rhesus monkeys can represent internally the invisible displacements of a moving target in target prediction tasks, why then do monkeys fail on invisible displacement tasks used in object permanence research (deBlois & Novak, 1994)? The answer to this question is as yet unclear, but we have some tentative suggestions with regard to differences in task demand and the experience of the subjects used.

Task demand. The target prediction and object permanence paradigms may likely require subjects to use different information. In target prediction tasks, subjects need to respond in anticipation of target movement, whereas subjects in invisible displacement tasks need to reconstruct the path of object movement. This difference in prospective and retrospective processing (Dumas, 1992) may require subjects to utilize different information (but see Goulet, Dore, & Rousseau, 1994).

Alternatively, the HOLE and LASER tasks seem to be more participatory for the monkeys than object permanence tasks. Our subjects, when they chose to work, were at every point involved in the task. That is, they were not required to observe a sequence of events passively and then make a response, but they were actively involved in the process of each task: trying to catch a moving target or trying to fire a shot at a moving target. Because the HOLE and LASER tasks are inherently dynamic (i.e., moving) tasks, the monkeys likely had more opportunity to learn about the dynamics of stimulus movement and, hence, the properties of occlusion. Washburn (1993) noted that tasks with moving as opposed to stationary stimuli seem to improve performance because they present more of a challenge to the monkeys and result in increased attention. This may have contributed further to the monkeys' performance in our set of experiments.

The possibility that differences in task demand may influence the solution of an invisible displacement problem suggests that the ability to represent invisible displacement may be constrained by other cognitive variables; that is, it may not be as general or robust a capacity (at least at certain points of ontogenetic or phylogenetic development) as traditionally thought. Because the object permanence paradigm has been the only paradigm used to define invisible displacement and to test subjects' ability to infer it, it is not clear that rhesus monkeys' failure on invisible displacement tasks is due to a complete lack of representational capacity (Dumas, 1992; Natale & Antinucci, 1989). Infants who appear to be able to solve invisible displacement tasks do not necessarily solve all types of transposition problems, the solutions of which are also believed to rest on the ability to represent unseen movement. In studying infants' performance on invisible displacement and transposition problems, Sophian (1985) suggested that attentional factors may contribute to the difficulty that infants experience on some transposition problems. Performance on object permanence tasks has often been found to be differentially affected by the type of container used to transfer the food object, the type of occluder used, the depth of the occlusion, and even the testing environment (see Bremner, 1985, for review). Furthermore, Baillargeon's (1986, 1987) creative use of different testing procedures has led to results that put into question the relatively late age at which Piaget (1954) asserted object permanence to be possessed. Hence, the expression of representational capacity may be constrained by other cognitive or perceptual processes as evidenced through performance in tasks with different demands.

Subject variables. Washburn and Rumbaugh (1991b) noted that training and testing rhesus macaques on the computer-testing paradigm rather than with traditional, manual procedures has resulted in previously unprecedented performance on a variety of tasks. Learning set, transfer index, and mediational scores were both reliably higher and qualitatively different for the monkeys on the LRC-CTS than with those studied previously with the Wisconsin General Testing Apparatus (WGTA; e.g., Harlow, 1949). That is, the rhesus monkeys evidenced a capacity for relational learning, whereas prior research had defined the species as restricted to associative learning (see Washburn & Rumbaugh, 1991b, for a discussion of these issues). Such a result is made even more surprising given that LRC-CTS training requires the monkeys to overcome the problems of spatial discontiguity and the use of computer-generated, planimetric stimuli. Both of these obstacles have resulted in compromised learning by rhesus macaques and other monkey species tested in traditional paradigms (e.g., Meyer, Treichler, & Meyer, 1965).

Washburn and Rumbaugh (1991b) suggested that the improved performance of the monkeys may be due to several factors that are inherent in the LRC-CTS procedure, such as (a) the ability to reduce the intertrial interval, which improved transfer in the mediational task, and (b) allowing subjects to work at their own pace, which may have resulted in performing on the tasks at times when their motivation to work and attention was high. As important, however, is the suggestion that extensive experience with the CTS has resulted in qualitative shifts in the capabilities of the test-wise rhesus monkeys. Those monkeys have demonstrated numerous competencies that were previously believed to be unique to humans and apes (e.g., target prediction, symbol learning, perceived control, and Stroop-like effects).

The streamlined nature of the LRC-CTS and the unique testing environment that it affords may have contributed to the qualitatively different performance the monkeys in our HOLE and LASER experiments demonstrated compared with previous studies (e.g., deBlois & Novak, 1994). It is also likely, however, that extensive LRC-CTS experience may have simply evoked qualitatively different performance capabilities from the rhesus macaques in our experiments. As a result, monkeys with extensive experience with the CTS may be more likely to infer invisible displacement than the rhesus macaques in other experiments. Whether or not the CTS-trained rhesus can infer invisible displacement outside the context of the computerized testing system is an interesting question to pursue in future research.

Paradigmatic Alternatives

The results of our experiments reflect the great potential that the computerized target prediction paradigm holds for investigating movement representation in human and nonhuman primates. As is evident from the variety of tasks used to test object permanence in humans, the use of the object permanence paradigm on nonhuman primates, though extremely valuable, needs to be augmented with other testing paradigms. By doing so, a better understanding of the varied manifestations of movement representation can be gained. More investigation is needed to understand the constraints on the expression of representational capacity, the experience that may or may not be required for such an expression, and the nature of the representation itself.

In conclusion, the nature of our tasks, use of a computerized testing paradigm, and the experience of the monkeys seem to have opened the door to elucidating their ability to represent internally the invisible displacements of a moving target. From the results of this study and those of object permanence studies, it seems likely that representing invisible displacement may not be a binary capacity, which one has or does not have, but rather is a capacity that might be more or less general depending on the species and, hence, more or less sensitive to particular task demands. Rhesus macaques apparently function under particular constraints which the WGTA-based object permanence paradigm has not, heretofore, been able to circumvent.

References

Baillargeon, R. (1986). Representing the existence and the location of hidden objects: Object permanence in 6- and 8-month-old infants. *Cognition, 23,* 21–41.

Baillargeon, R. (1987). Object permanence in 3½- and 4½-month-old infants. *Developmental Psychology, 23,* 655–664.

Bremner, G. J. (1985). Object tracking and search in infancy: A review of data and a theoretical evaluation. *Developmental Review, 5,* 371–396.

deBlois, S. T., & Novak, M. A. (1994). Object permanence in rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology, 108,* 318–327.

Dore, F. Y., & Dumas, C. (1987). Psychology of animal cognition: Piagetian studies. *Psychological Bulletin, 102,* 219–233.

Dumas, C. (1992). Object permanence in cats (*Felis catus*): An ecological approach to the study of invisible displacement. *Journal of Comparative Psychology, 106,* 404–410.

Etienne, A. S. (1984). The meaning of object permanence at different zoological levels. *Human Development, 27,* 309–320.

Finke, R. A., Freyd, J. J., & Shyi, G. C.-W. (1986). Implied velocity and acceleration induce transformations of visual memory. *Journal of Experimental Psychology: General, 115,* 175–188.

Freyd, J. J., & Finke, R. A. (1984). Representational momentum. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 10,* 126–132.

Gallistel, C. R. (1990). *The organization of learning.* Cambridge, MA: MIT Press.

Goldberg, S. (1976). Visual tracking and existence constancy in 5-month-old infants. *Journal of Experimental Child Psychology, 22,* 478–491.

Goulet, S., Dore, F. Y., & Rousseau, R. (1994). Object permanence and working memory in cats (*Felis catus*). *Journal of Experimental Psychology: Animal Behavior Processes, 20,* 347–365.

Harlow, H. F. (1949). The formation of learning sets. *Psychological Review, 56,* 51–65.

Harris, P. L. (1987). The development of search. In P. Salapatek & L. Cohen (Eds.), *Handbook of infant perception: Vol. 2. From perception to cognition* (pp. 155–207). New York: Academic Press.

Krushinsky, L. V. (1990). *Experimental studies of elementary reasoning: Evolutionary, physiological and genetic aspects of behavior* (E. Tobach & I. Poletaeva, Trans). New Delhi, India: Amerind Publishing. (Original work published 1977)

Meyer, D. R., Treichler, F. R., & Meyer, P. M. (1965). Discrete trial training techniques and stimulus variables. In H. Schrier, H. F. Harlow, & F. Stollnitz (Eds.), *Behavior of nonhuman primates, 1* (pp. 1–49). New York: Academic Press.

Natale, F., & Antinucci, F. (1989). Stage 6 object-concept and representation. In F. Antinucci (Ed.), *Cognitive structure and development in nonhuman primates* (pp. 97–112). Hillsdale, NJ: Erlbaum.

Neiworth, J. J., & Rilling, M. E. (1987). A method for studying imagery in animals. *Journal of Experimental Psychology: Animal Behavior Processes, 3,* 203–214.

Nelson, K. E. (1971). Accommodation of visual-tracking patterns in human infants to object movement patterns. *Journal of Experimental Child Psychology, 12,* 182–196.

Piaget, J. (1954). *The construction of reality in the child.* New York: Basic Books.

Rumbaugh, D. M., Richardson, K. W., Washburn, D. A., Savage-Rumbaugh, S. E., & Hopkins, W. D. (1989). Rhesus monkeys

(*Macaca mulatta*), video tasks, and implications for stimulus-response spatial contiguity. *Journal of Comparative Psychology, 103,* 32–38.

Sophian, C. (1985). Understanding the movements of objects: Early developments in spatial cognition. *British Journal of Developmental Psychology, 3,* 321–333.

Vauclair, J., Fagot, J., & Hopkins, W. D. (1993). Rotation of mental images in baboons when the visual input is directed to the left cerebral hemisphere. *Psychological Science, 4,* 99–103.

Washburn, D. A. (1992a). Analyzing the path of responding in maze-solving and other tasks. *Behavior Research Methods, Instruments, & Computers, 24,* 248–252.

Washburn, D. A. (1992b). Human factors with nonhumans: Factors that affect computer-task performance. *International Journal of Comparative Psychology, 5,* 191–204.

Washburn, D. A. (1993). The stimulus movement effect: Allocation of attention or artifact? *Journal of Experimental Psychology: Animal Behavior Processes, 19,* 380–390.

Washburn, D. A., & Rumbaugh, D. M. (1991a). Impaired performance from brief social isolation of rhesus monkeys (*Macaca mulatta*): A multiple video-task assessment. *Journal of Comparative Psychology, 105,* 145–151.

Washburn, D. A., & Rumbaugh, D. M. (1991b). Rhesus monkeys (*Macaca mulatta*) complex learning skills reassessed. *International Journal of Primatology, 12,* 377–388.

Washburn, D. A., & Rumbaugh, D. M. (1992). A comparative assessment of psychomotor performance: Target prediction by humans and macaques. *Journal of Experimental Psychology: General, 121,* 305–312.

Washburn, D. A., & Rumbaugh, D. M. (1994). Training rhesus monkeys (*Macaca mulatta*) using the computerized test system. In J. R. Anderson, J. J. Roeder, B. Thierry, & N. Herrenschmidt (Eds.), *Current primatology: Volume III. Behavioral neuroscience physiology & reproduction* (pp. 77–83). Strasbourg, France: Universite Louis Pasteur.

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