Journal of Comparative Psychology
2006, Vol. 120, No. 3, 314–321

0735-7036/06/$12.00 DOI: 10.1037/0735-7036.120.3.314

Searching Beneath the Shelf in Macaque Monkeys: Evidence for a Gravity Bias or a Foraging Bias?

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The reasons underpinning search biases in 2 species of macaque monkeys (*Macaca mulatta* and *Macaca arctoides*) were explored over the course of 3 experiments requiring monkeys to search for a hidden food reward. The results reveal that monkeys are adept at exploiting perceptual cues to locate a food reward but are unable to use physical constraints such as solidity as cues to the reward's location. Monkeys prefer to search for a food reward beneath a solid shelf, not because they have an expectation that the reward should be there, but rather because, in the absence of usable cues, this bias emerges as a default search option. It is hypothesized that this bias may have its roots in a history of competition for food resources.

Keywords: invisible displacement, search biases, gravity error, understanding of solidity, looking–searching dissociation

The gravity error, identified and so-called by Hood (1995), has aroused much interest and investigation, not only in the developmental field (e.g., Hood, 1995, 1998; Cummins-Sebree, 2004) but also within the comparative field, with a number of researchers identifying the error to varying degrees in a number of nonhuman species (Cacchione & Burkart, 2005 [*Callithrix jacchus*]; Hood, Hauser, Anderson, & Santos, 1999 [*Saguinus oedipus*]; Osthaus, Slater, & Lea, 2003 [*Canis familiaris*]; Southgate, 2005 [*Macaca mulatta*]; Tomonaga, Imura, Mizuno, & Tanaka, 2005 [*Pan troglodytes*]. The error is observable when a reward is dropped down an S-shaped opaque tube. Rather than searching for the reward at the end of the tube, these species make the error of searching directly beneath the top of the tube. One proposed explanation for this error is that it reflects a naïve theory of the effect of gravity; that all falling objects fall straight down (Hood, 1995). In committing this error, subjects search in accord with this principle and fail to take into account mediating factors, such as the presence of a solid tube.

The extent to which the proposed gravity error might impinge on search for objects that have disappeared from view was highlighted by Hauser (2001) when a different search error was identified on another task and subsequently attributed to another dimension of this same gravity bias. This task, originally designed by Spelke and colleagues (Spelke, Breinlinger, Macomber, & Jacobson, 1992), involved presenting rhesus macaques with two search containers, one above and one beneath a solid shelf. A screen was erected in front of the apparatus and an object dropped from above. Hauser (2001) found that, rather than searching in the cup on top of the shelf, monkeys searched predominantly in the lower search location, beneath the solid shelf. This bias toward the lower search container led to the proposal that this preference reflects a gravity bias. Not only is there an expectation that all falling objects will fall in a straight line (as evidenced by the search error seen on the tubes task), but these subjects also expect that any falling object will fall to the lowest possible point.

According to Hauser (2001), this prepotent expectation can override knowledge about physical constraints (in this case, solidity) that monkeys *do* possess. In a control condition, two boxes were placed horizontally side by side and a screen was placed in front of the boxes such that the monkeys could no longer see them. A reward was then rolled from one side behind the screen. Hauser found that monkeys searched predominantly in the first box, suggesting that monkeys do have the ability to take into account physical constraints. They reason correctly that the reward could not have passed through the first box and into the second, and so they direct their search toward the first box. It is the additional element of gravity, it is argued, that is introduced when the task is presented vertically that leads to the monkeys' failure on the vertical task.

The experiments reported here were designed to elucidate the reasons why monkeys might choose to search under the shelf, and specifically to address the proposal by Hauser (2001) that search on his task reflects a naïve theory of gravity that all falling objects fall to the lowest point. A problem with this interpretation of monkeys' behavior is that searching in the near box on the horizontal control does not necessarily show that monkeys have the understanding of solidity that would enable them to pass the vertical task were it not for the introduction of the gravity problem. Monkeys may simply have a preference for searching in a location closest to the disappearance of an object, a behavior that has been noted in both monkeys and cats (Goulet, Doré, & Rousseau, 1994;

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We thank the technicians at the School of Psychology Animal House, University of St. Andrews, and at the Medical Research Council Human Reproductive Sciences Unit, for their support in carrying out these studies. We also thank Gergely Csibra for helpful comments on this article.

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Santos, 2004) and one that would lead them to serendipitous success on this particular control without the need to attribute any understanding of the physical constraints of the task. The first experiment reported here was designed to test whether macaque monkeys do exhibit a *proximity* bias when presented with a similar task.

The second and third experiments reported were designed to address a possible alternative explanation for why monkeys make the error of searching for a falling object beneath a shelf. We propose that monkeys may have a more general bias to search under a shelf irrespective of what kind of movement they encounter. On the basis of a proposal by Karin-D'Arcy and Povinelli (2002) that evolutionary pressures have led monkeys to prefer to forage for food in sheltered places to avoid competition from conspecifics and predation from other species, we raise the possibility that monkeys may approach a task like this with a preexisting bias to search below the shelf for a food reward. If this were the case, the preference that monkeys exhibit for choosing the location beneath the shelf does not reflect a naïve theory about gravity, but rather a long history of competition and predation that has led animals to develop a bias toward feeding in perceived "safer" locations.

Experiment 1

The aim of Experiment 1 was to test the prediction that monkeys will search in the location closest to the disappearance of a reward, irrespective of any physical constraints that would prevent the reward from being there. We present monkeys with a task in which, for one condition, searching in the closest location is correct but for another condition this is the incorrect response. If monkeys search with an indiscriminate proximity bias, they should pass one condition but fail the other.

Method

Subjects. Ten adult monkeys participated: 4 rhesus (*Macaca mulatta*) and 6 stumptail macaques (*Macaca artoides*). Both groups of monkeys were housed in small groups for breeding and had only a little experience of testing prior to participating in this experiment.

Apparatus. The apparatus used in the present experiment is pictured in Figures 1a and b. Blue plastic rings containing wood shavings were used as the search locations; the monkeys had experienced these rings as search locations in one previous experiment (Southgate, 2005). A rectangular piece of wood measuring 50 cm × 40 cm served as the base for the search containers. Metal slots for holding in place an opaque black screen (30 cm × 25 cm) and a ramp ran along each side of the rectangular base, as well as a piece that connected the two longer sides together in the middle. To prevent monkeys using the sound made by the food rewards as they fell into the wood shavings, we prebaited the correct location before each trial. The food reward that the monkey saw rolling down the ramp instead rolled into a concealed tray on the back of the opaque screen, and the tray contained cotton wool to mask any sound. A removable sloping ramp made out of polycarbonate and painted black could slot into the base. The ramp measured 20 cm at its highest point, 15 cm at its lowest point, and had a width of 15 cm. The ramp also had a groove running its entire length so that the food reward would roll in a straight line. The apparatus had secure fastenings in place that screwed into the plastic search rings to prevent the monkey from removing them. These could easily be moved from trial to trial so that the search locations could be correctly placed for each trial. Grapes and chocolate-covered candies were used as food rewards.

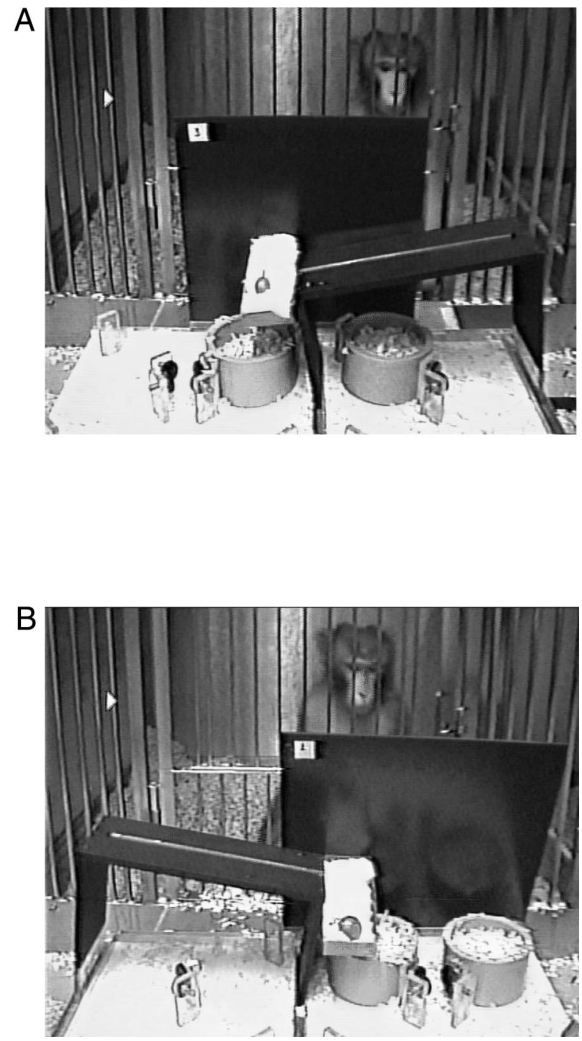


Figure 1. Apparatus used in Experiment 1 for (a) *under* trials and (b) *after* trials. The correct container for the trial type is prebaited with a food reward. The same type of reward is then rolled from the top of the ramp and lands in the secret container attached to the back of the screen. The screen is removed and the monkey is allowed to search.

Design and procedure. There were two types of trials (named for the position of the incorrect container relative to the ramp): *under* trials in which one container was placed at the end of the ramp and the other was placed directly underneath the ramp, either from the left side or the right side of the ramp (Figures 2a and 2b), and *after* trials in which both hiding containers were placed, one after the other at the end of the ramp, again with the ramp positioned from left to right or from right to left (Figures 2c and 2d). A maximum of 12 trials were carried out per subject in three blocks of 4 trials: *under* trial, left; *under* trial, right; *after* trial, left; and *after* trial, right. The event was designed to be presented from either the left or right to avoid the potentially confounding effects of handedness.

The test monkey was isolated for testing, and the experimenter was seated opposite the monkey on a small stool or stood opposite the monkey (depending on the particular monkey's home cage). Prior to the onset of testing, each monkey was familiarized with the apparatus and the setup. The experimenter placed the ramp so that the end was facing the monkey and rolled a food reward from the top of the ramp toward the monkey five times. This familiarization was included so that the monkey could see what

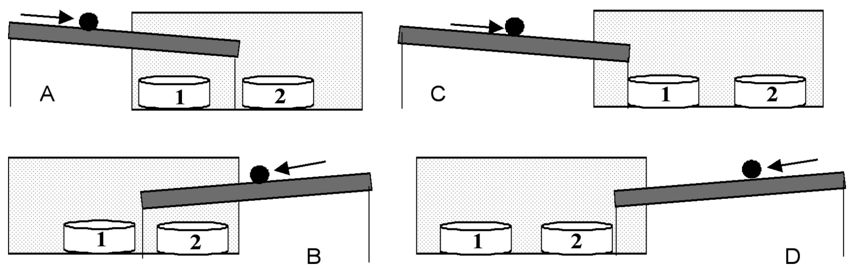


Figure 2. A and B: *Under* trials from the left and right, respectively. C and D: *After* trials from the left and right, respectively.

happens when a reward is rolled down the ramp. When testing commenced, the opaque screen was slid into place to occlude the two search containers but leaving the top half of the ramp visible. A food reward was placed at the top of the ramp and after the experimenter had drawn the subject's attention to the reward, it was released and rolled down the ramp, disappearing behind the screen. The screen was then removed and, in the case of *under* trials, the experimenter slid back the ramp to allow the monkey equal access to both search locations. Monkeys were allowed to search until they found the reward.

Results and Discussion

On *after* trials, the correct location is always the nearest box to the point of disappearance of the object, and so if subjects are using a search-nearest-box rule, they should choose the first box significantly more often than the second. On *under* trials, the correct location is always the furthest box (because the object could not be in the first box without passing through the solid shelf), but if subjects are using this search-nearest-box rule, they should fail *under* trials.

Seven monkeys completed 12 trials (6 *after* trials and 6 *under* trials), 2 completed 11 trials, and 1 completed 9 trials. The mean proportion of correct first searches on both *after* and *under* trials was calculated (see Figure 3). The mean proportion of correct first searches on *under* trials was 17.6% and on *after* trials was 81.9%. The proportion of correct searches on *after* and *under* trials was then subdivided into side of presentation. A $2 \times 2 \times 2$ repeated measures analysis of variance (ANOVA) with condition (*after* trials vs. *under* trials) and side (left vs. right presentation) as within-subjects variables and species (rhesus vs. stumptail macaque) as a between-subjects variable revealed a significant main effect of condition, $F(1, 8) = 27.3$, $p \leq .001$, $\eta p^2 = .773$. Monkeys performed better on *after* trials than *under* trials. This finding was confirmed with a nonparametric Wilcoxon's test ($Z = 2.81$, $p \leq .005$). There was no effect of side of presentation or species. One-sampled t tests indicate that monkeys perform significantly below chance on *under* trials, $t(9) = 6.20$, $p \leq .001$, and significantly above chance on *after* trials, $t(9) = 5.98$, $p < .001$.

In accord with the predicted result, monkeys searched in the location nearest to where the reward disappeared, irrespective of the possibility of the reward being at that location. The above-chance performance of monkeys on the *after* trials gives the impression of an understanding of the task, but when taken in the context of the very poor performance on the *under* trials, it is clear that this above-chance performance is not reflective of any real understanding of where the reward can be. As such, Hauser's (2001) claim that monkeys on his task showed an understanding of solidity that was only surpassed on the vertical condition by the additional troublesome gravity component must be taken with caution.

Experiment 2

The aim of Experiment 2 was to explore whether monkeys may have a preference for the beneath-shelf location, in the absence of any physical constraints that should lead them to search in one location over the other. Such a preference may reflect the presence

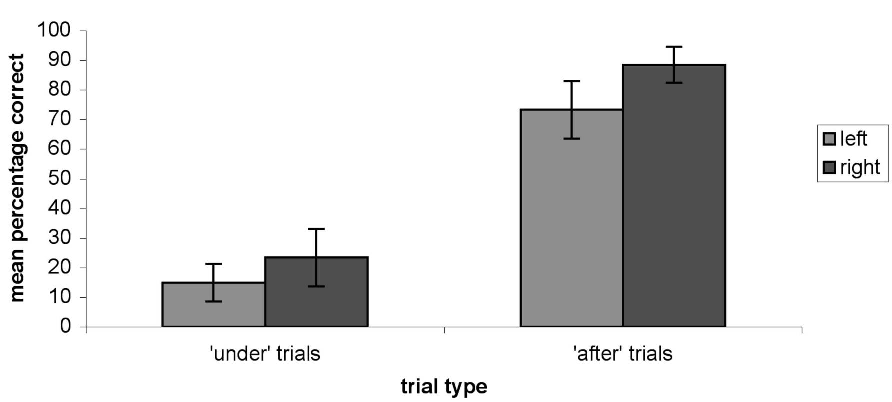


Figure 3. Mean ($\pm$ *SE*) percentage of correct trials as a function of the type of trial (under vs. after) and the side of presentation (left vs. right).

of a foraging bias that might explain why monkeys search underneath a solid shelf for a food reward. Monkeys were presented with two identical food rewards, one placed on top of the shelf and one placed directly below. Because there are no physical constraints or other cues that determine one location as a more preferable place to search than the other, we reasoned that any consistent order in which monkeys took the two food rewards would highlight any location preference they may have.

Method

The 4 rhesus monkeys that took part in Experiment 1 plus an additional 4 rhesus monkeys were subjects in Experiment 2. A wooden shelf measuring 27 cm in height by 40 cm in width was used as well as an opaque black screen that could occlude the apparatus (measuring 47 cm × 25 cm).

As in Experiment 1, the experimenter sat opposite the isolated monkey and placed the shelf in front of the monkey. The experimenter then placed the opaque screen in front of the apparatus so that the edges of the shelf were still visible to the subject (see Figure 4). From the back of the apparatus, the experimenter then placed two identical food rewards behind the screen, one above the shelf and one below. The screen was then removed, and the monkey was able to take the fully visible food rewards. Each monkey participated in up to 12 trials.

Results and Discussion

The food reward that the monkey took first was the variable of interest. The percentage of above-shelf-first versus beneath-shelf-first responses per monkey was calculated. Seven out of 8 monkeys took the food reward beneath the shelf first more often than taking the food reward above the shelf. One monkey showed the reverse pattern of search. The mean percentage of first choices directed above the shelf was 22%, whereas the mean percentage of first choices directed beneath the shelf was 78%. A one-sampled t test on this percentage data shows that, as a group, the monkeys preferred to take the food reward beneath the shelf before taking the reward above the shelf, more often than would be expected by chance, $t(7) = 2.69$, $p \leq .05$.

No monkey avoided taking the food reward located on top of the shelf (after the food under the shelf had been taken), indicating that there was nothing aversive about this location. The results suggest that, all things being equal, rhesus monkeys have a bias toward taking a food reward from beneath a solid shelf. Two factors can create a situation in which neither search location is perceived as intrinsically more likely to contain the reward than the other. First, as is the case in this preference test, the fact that the two rewards are identical meant that only the monkey's location preference could determine their first search. Second, if the reward is not visible, as is the case in an invisible displacement, an inability to represent the invisible displacement of the reward may create a situation in which neither location is perceived as more likely than the other to contain the food reward. Experiment 3 presented the same subjects with an invisible displacement test in which one of the two search locations could not contain the object because it is located underneath the solid shelf.

Experiment 3

If the monkey understands that a solid shelf constrains the falling object's pathway, then this would render the top location more likely to contain the reward and therefore create an inequality between the two search locations. On the other hand, if the monkey is unable to correctly reason about the effect of a solid shelf on the reward's trajectory, both locations may be perceived as equally likely to contain the reward. However, the presence of discernible spatial cues may provide the monkey with an alternative cue to the reward's location and, even if unable to reason about physical constraints, the information provided by spatial cues may create an inequality between the two locations such that the monkey now perceives one location as more likely to contain the food reward than the other. For example, in controls used in Hauser's (2001) series of experiments, monkeys were able to correctly locate the reward in situations in which the two search locations were misaligned but not when they were aligned.

The present study was designed to investigate whether a beneath-shelf bias is exhibited in an invisible displacement task in which there is no difference between the two search locations in terms of gravitational plausibility. In other words, if monkeys really do have a naïve theory of gravity in which they expect all falling objects to fall to the lowest point, then, if both search locations are on the same level, both are equally plausible. If monkeys continue to display a preference for a search location

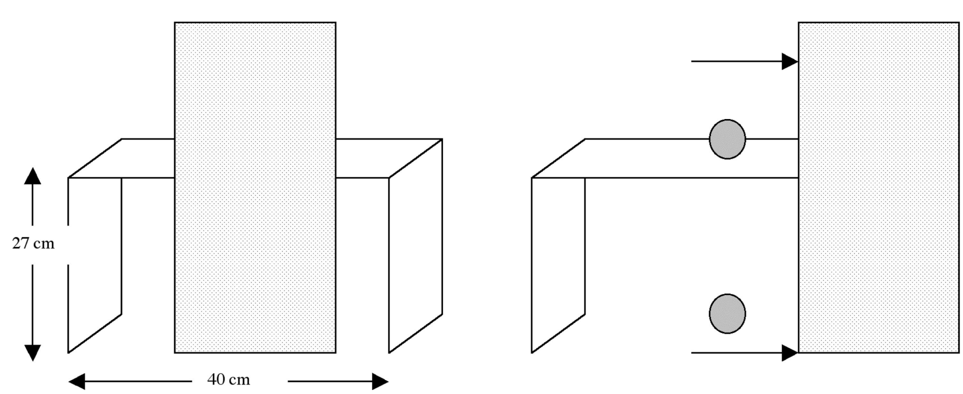


Figure 4. Diagram showing apparatus used in Experiment 2. With an occluding screen in place, an identical food reward is placed above and beneath a wooden shelf. Then the screen is then removed and the monkey is allowed to search.

beneath a solid shelf even when both locations fit equally with an expectation that falling objects fall to the lowest point, then it is unlikely that a beneath-shelf bias can be attributable to a naïve theory of gravity.

To test this prediction, we designed an experiment in which two cups were placed on either side of a solid shelf, so that one cup was underneath the shelf and the other cup was on the outside of the shelf (see Figure 5). The distance between the outside cup and the inside cup was varied systematically. On the basis of findings by Hauser (2001) and the findings of Experiment 2 of this article, it was predicted that monkeys would show a beneath-shelf bias in the absence of sufficient spatial cues to delineate the two search locations (i.e., when the two search locations are very close together) but that this bias would disappear when spatial cues became useful (i.e., when the cups are further apart). A control condition involved the shelf being removed so that there were no differences in the appeal of either cup. The control condition was included to ensure that there was no intrinsic preference for the outside as opposed to the inside cup. In the absence of the shelf, when the two search locations are close together and there are therefore no spatial cues available as to the location of the object, search should be random.

Method

Subjects and apparatus. The same 8 rhesus macaques that took part in Experiment 2 also took part in Experiment 3. The same shelf and opaque screen used in Experiment 2 were also used in Experiment 3. In addition, two plastic colored cups were used as hiding containers. These cups measured 15.5 cm in height, and cotton wool was placed inside each cup to eliminate any auditory cues as the food reward fell into the cup.

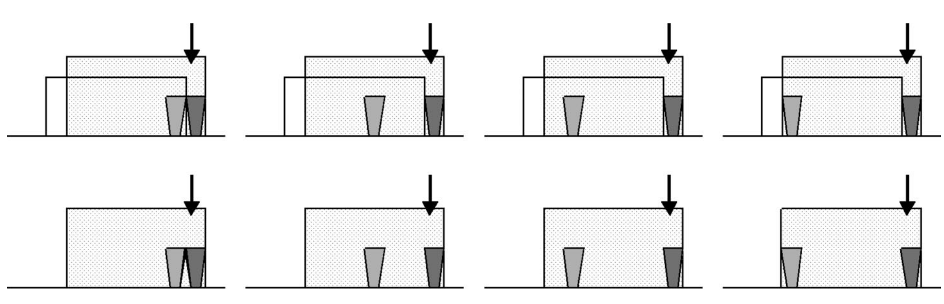
Design and procedure. With the experimenter sitting opposite, monkeys were again presented with the same wooden shelf. Experiment 3 comprised four possible paired-container configurations. In the Configuration 1, the two cups were placed directly adjacent to each other, separated only by one of the walls of the shelf and thus spatially undifferentiated. In Configurations 2, 3, and 4, the cup placed under the shelf was increasingly further away from the cup on the outside of the shelf. The distances between cups, measured from the center of one cup to the center of the other cup, were 11 cm, 18 cm, 27 cm, and 35 cm for Configurations 1, 2, 3, and 4, respectively. These spatial positions were marked so the experimenter knew where to place the cups. Monkeys were presented with each of these four configurations twice from the right (i.e., the outside cup was placed on the right side of the shelf and each of the inside cups was moved further to the left depending on the configuration chosen) and twice from the left (i.e., the outside cup was placed on the left side of the shelf and each of the inside cups was moved further to the right depending on the configuration chosen). Subjects might choose a particular location because it is ipsilateral to their dominant hand, and so presenting the task from both sides removed this potentially confounding variable.

There were two conditions: shelf-present and shelf-absent. In the *shelf-present* condition, monkeys were presented with the wooden shelf and any of the four configurations of cups described above. A black screen was placed in front of the shelf, and a food reward was dropped from above into the outside cup. The screen was then removed, and monkeys were allowed to search in one cup. If they failed to find the reward on their first attempt, the second cup was removed. This aspect of the design was chosen to increase the monkey's motivation to search correctly rather than just relying on a search-all-containers strategy. In the *shelf-absent* condition, the paired-cups configurations were as above but no shelf was present. Each monkey received a total of 32 trials: 8 shelf-present trials (with 2 trials for each paired configuration) from the right; 8 shelf-present trials from the left; 8 shelf-absent trials from the right; and 8 shelf-absent trials from the left. The order of presentation of the trials was randomized for each monkey.

Results and Discussion

Each monkey completed the 32 trials. A mean percent correct score for each monkey was obtained for each of the 8 trial types (4 shelf-absent trials, 2 of each configuration and 4 shelf-present trials, 2 of each configuration; see Figure 6).

A 2 × 4 × 2 repeated measures ANOVA with shelf (shelf present vs. shelf absent), configuration (positions 1, 2, 3 and 4), and side of presentation (left vs. right) all as within-subjects factors, revealed a significant effect of configuration, $F(3, 21) = 8.45$, $p \leq .001$, $\eta_p^2 = .547$, and an effect of shelf that approached significance, $F(1, 7) = 4.57$, $p = .07$, $\eta_p^2 = .395$. In addition, the interaction between shelf and configuration also approached significance, $F(3, 21) = 2.58$, $p = .08$, $\eta_p^2 = .269$. Performance did not differ significantly with side of presentation. In line with our predictions, four planned comparisons were carried out to compare the effect of the shelf on each of the different configurations, collapsing the data over side of presentation. There was a significant difference in performance between shelf-present Configuration 1 trials and shelf-absent Configuration 1 trials, $t(7) = 3.27$,



1 **2** **3** **4**

Figure 5. Apparatus and conditions for Experiment 3. The upper row indicates the shelf-present condition, Configurations 1–4, and the lower row indicates the shelf-absent condition, Configurations 1–4. The food is always dropped into the outer container, and the position of the outer container was varied, half the time being to the right and half to the left of the shelf.

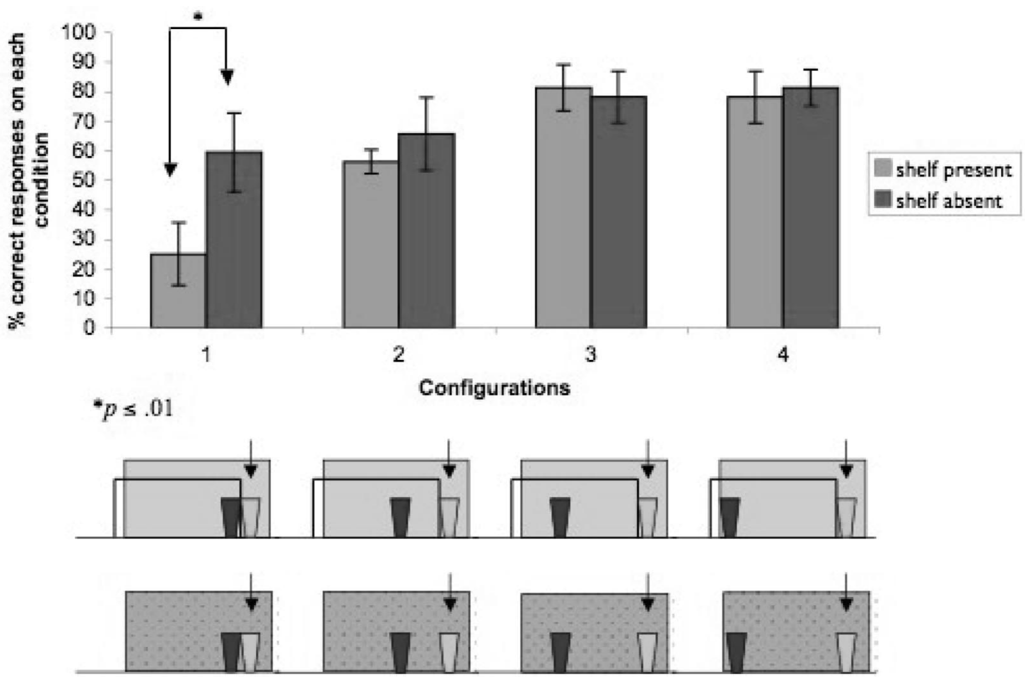


Figure 6. Mean (± *SE*) percentage of correct responses on each condition for Experiment 3.

$p \leq .01$, with monkeys performing significantly better on shelf-absent Configuration 1 trials. This conclusion was confirmed in a nonparametric Wilcoxon's test ($Z = 2.46$, $p \leq .01$). Performance on shelf-absent Configuration 1 trials was not better than would be expected by chance, but performance on shelf-present Configuration 1 trials was significantly worse than would be expected by chance, $t(7) = 2.37$, $p \leq .05$, indicating that monkeys chose the cup beneath the shelf more than would be expected by chance.

The significant main effect of configuration indicates that when containers are in close proximity such that monitoring the position from which the reward is dropped is unhelpful in providing a cue to the correct container, monkeys choose randomly between the two containers. However, the addition of a solid shelf results in monkeys' performance dropping below chance, presumably because they prefer to take the container underneath the shelf.

When spatial cues are unambiguous (i.e., in Configurations 3 and 4), it appears that the tendency to choose the container beneath the shelf can easily be overridden. This ability to override the tendency to choose the container beneath the shelf is also evident in Hauser's (2001) third experiment showing that when the top and bottom containers are significantly misaligned in relation to one another, allowing spatial cues to be exploited, monkeys do not show a bottom-box bias.

The results from this experiment clearly demonstrate that rhesus monkeys have a preference for searching for food in a beneath-shelf location, and this does not seem to be related to a naïve theory of gravity. Rather, in the absence of usable information as to the reward's location, monkeys will choose a cup based on their preference for location and not on the possibility of that location containing the reward. Moreover, these results reveal another situation in which monkeys seem unable to take into account the constraint that the solid shelf has on the object's pathway. They appear not to understand that a falling object cannot pass through a solid shelf and into a cup beneath. The results from the control condition suggest that it is the presence of the shelf that creates a bias for the inside cup, and that when there are spatial cues to delineate the object's location, the presence of the shelf no longer exerts an influence on search.

General Discussion

The results from the experiments presented in this article confirm that monkeys do exhibit a bias toward searching underneath a solid shelf for a food reward. However, we do not believe that this bias is reflective of a naïve theory about the effects of gravity. We propose that monkeys approach the task with a bias that arises in search behavior when the monkey has no exploitable cues as to the rewards' location. Monkeys show no evidence of being able to exploit physical cues such as solidity to locate a food reward (Experiment 1), and as such the presence of the solid shelf in Experiment 3 does not serve to aid them in locating the food. They rely on perceptual cues where available, but in their absence, they resort to a beneath-shelf bias.

One possible reason why monkeys show a preference for searching for or taking a reward from underneath a solid shelf is because their search is driven by a desire to avoid food that is out in the open. A similar phenomenon was described by Karin-D'Arcy and Povinelli (2002) with respect to chimpanzees. In the shelf paradigm, the beneath-shelf location is the more sheltered, less exposed location, and it may be this that biases subjects to prefer to take a reward from beneath the shelf. Recent work by Flombaum and Santos (2005) suggests that even rhesus macaques who are well habituated to the presence of, and provisioned by humans, do still view humans as "competitors" in situations involving food and prefer to steal food from a human whose gaze is directed away from the desired food item than the human whose gaze is not. This suggests that the visibility of food to others might influence a rhesus monkey's disposition to search for it.

Behavioral biases appear common, especially in the developmental literature. As previously mentioned, Hood (1995) reported that young children show a bias toward searching in a straight-down location on the tubes task, and in a different search task, Mash, Keen, and Berthier (2003) reported that children exhibit a center-response bias in which they direct most of their searches toward the center of the apparatus than at the periphery. An important question is under what conditions do such biases arise? Does the bias, as Hood proposed is the case for the gravity error, mask correct knowledge about where the object really is? Or do these biases emerge in behavior as default responses when the subjects cannot formulate a correct response because they cannot ascertain the location of the reward? We believe that the results from the current study point toward a bias that emerges as a default rather than one that masks correct knowledge. As the results show, monkeys can very easily overcome this bias when they have other cues as to the reward's location (such as spatial separation), and it is possible that, had we placed a more desirable food reward on the top of the shelf in the preference test, this bias would have disappeared. On the other hand, a bias that governs behavior to such an extent that it masks correct knowledge would likely be much more difficult to overcome.

The bias exhibited by monkeys on the current invisible displacement task appears to arise in the absence of perceptual cues that the monkey can exploit to find the food reward. As such, it seems that monkeys are unable to take into account physical constraints to reason about the rewards' location. This finding fits with much previous work on monkeys' understanding of invisible displacement. With the exception of just a few studies (e.g., Mendes & Huber, 2004; Neiworth et al., 2003; Wise, Wise, & Zimmerman, 1974), the majority of studies have found that monkeys have great difficulty with invisible displacement tasks when the appropriate controls are put in place (De Blois & Novak, 1994; De Blois, Novak, & Bond, 1998; Natale, Antinucci, Spinozzi, & Poti, 1986). Monkeys appear able to solve the tasks when they can exploit subtle cues and rules but are unable to find the food reward when such rules are eliminated and reasoning and true understanding are required (Doré & Dumas, 1987).

Although it is clear from the current study that monkeys do not take into account the physical constraints of solidity to solve the task, there is nevertheless evidence that, under certain conditions, they do recognize when such constraints have been violated. Using the same paradigm as was used by Hauser (2001), Santos and Hauser (2002) found that rhesus macaques looked longer when a food reward was revealed beneath the shelf rather than above the shelf. This increased attention to the "impossible" outcome was interpreted by the authors as evidence that rhesus macaques know something about the constraint of solidity on object movement. This interesting finding runs parallel to findings in the developmental literature that have shown numerous cases of young infants looking longer toward impossible outcomes that violate laws of physics (e.g., Spelke et al., 1992). However, this is in sharp contrast to recent findings showing that much older children show poor performance on tasks presented in the search domain that are purported to require the same knowledge of physical constraints for success. It would seem therefore that for both children and monkeys, any understanding that they have of physical constraints cannot be actively used to help them on a search task.

Arguably, one of the most important tasks in comparative and developmental psychology is to resolve this paradox. Can we really say that monkeys have knowledge of physical constraints if they do not demonstrate this knowledge on an explicit task? What is it that prevents them from translating the understanding they exhibit on looking tasks to the search domain? The studies reported in this article suggest that monkeys resort to strategies or biases in the absence of conceptual understanding, but what it is that prevents monkeys from using the kind of conceptual knowledge they demonstrate on looking tasks in search tasks awaits investigation.

References

Cacchione, T., & Burkart, J. (2005, April). *Is the gravity bias traceable by action only—or by perception as well?* Poster presented at the biennial meeting of the Society for Research in Child Development, Atlanta, GA.

Cummins-Sebree, S. (2004, May). *Core knowledge hypothesis vs. ecological theory: Understanding spatial reasoning development in 24–44-month-olds*. Poster presented at the International Conference on Infant Studies, Chicago.

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

De Blois, S. T., Novak, M. A., & Bond, M. (1998). Object permanence in orangutans (*Pongo pygmaeus*) and squirrel monkeys (*Saimiri sciureus*). *Journal of Comparative Psychology, 112,* 137–152.

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

Flombaum, J. I., & Santos, L. R. (2005). Rhesus monkeys attribute perceptions to others. *Current Biology, 15,* 447–452.

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

Hauser, M. D. (2001). Searching for food in the wild: A nonhuman primate's expectations about invisible displacement. *Developmental Science, 4,* 84–93.

Hood, B. M. (1995). Gravity rules for 2–4 year-olds? *Cognitive Development, 10,* 577–598.

Hood, B. M. (1998). Gravity does rule for falling events. *Developmental Science, 1,* 59–63.

Hood, B. M., Hauser, M., Anderson, L., & Santos, L. (1999). Gravity biases in a nonhuman primate? *Developmental Science, 2,* 35–41.

Karin-D'Arcy, M. R., & Povinelli, D. J. (2002). Do chimpanzees know what each other see? *International Journal of Comparative Psychology, 15,* 21–54.

Mash, C., Keen, R., & Berthier, N. E. (2003). Visual access and attention in two-year-olds' event reasoning and object search. *Infancy, 4,* 371–388.

Mendes, N., & Huber, L. (2004). Object permanence in common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology, 118,* 103–112.

Natale, F., Antinucci, F., Spinozzi, G., & Poti, P. (1986). Stage 6 object concept in nonhuman primate cognition: A comparison between gorilla (*Gorilla gorilla gorilla*) and Japanese macaque (*Macaca fuscata*). *Journal of Comparative Psychology, 100,* 335–339.

Neiworth, J. J., Steinmark, E., Basile, B. M., Wonders, R., Steely, F., & DeHart, C. (2003). A test of object permanence in a new-world monkey species, cotton top tamarins (*Saguinus oedipus*). *Animal Cognition, 6,* 27–37.

Osthaus, B., Slater, A. M., & Lea, S. E. G. (2003). Can dogs defy gravity? A comparison with the human infant and a non-human primate. *Developmental Science, 6,* 489–497.

Santos, L. R. (2004). "Core knowledges": A dissociation between spatiotemporal knowledge and contact-mechanics in a non-human primate? *Developmental Science, 7,* 167–174.

Santos, L. R., & Hauser, M. D. (2002). A non-human primate's understanding of solidity: Dissociations between seeing and acting. *Developmental Science, 5,* F1–F7.

Spelke, E., Breinlinger, K., Macomber, J., & Jacobson, K. (1992). Origins of knowledge. *Psychological Review, 99,* 605–632.

Southgate, V. (2005). *A Comparative Study of the Understanding of Invisible Object Displacements in Macaque Monkeys (macaca mulatta and arctoides) and Children.* Unpublished doctoral dissertation, University of St. Andrews.

Tomonaga, M., Imura, T., Mizuno, Y., & Tanaka, M. (2005). *Gravity bias in young and adult chimpanzees (Pan troglodytes): Tests with modified opaque-tubes task.* Manuscript submitted for publication.

Wise, K. L., Wise, L. A., & Zimmerman, R. R. (1974). Piagetian object permanence in the infant rhesus monkey. *Developmental Psychology, 10,* 429–437.

Received September 6, 2005
Revision received March 7, 2006
Accepted March 8, 2006 ■