Tests of planning and the Bischof-Köhler hypothesis in rhesus monkeys (*Macaca mulatta*)

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Introduction

Planning is a hallmark of human thinking. We often plan for our next meal, our next conference visit, and even for our retirement. Planning is essential to modern human life; without it we could not construct buildings, schedule appointments, or prepare as we do for the changing seasons. One aspect of these examples of planning is that a need or motivational state is anticipated, although it is not currently experienced. We plan for a meal even though we are not currently hungry, we stockpile firewood even when not currently cold, and we save for retirement even when currently employed. Suddendorf and Corballis (1997) suggested that this ability to plan for a motivational state one does not currently experience, a component of what they call "mental time travel", is a defining feature of planning and developed late in hominoid evolution.

The idea that nonhuman animals have little or no capacity to plan for the future has been put forward many times (see Roberts, 2002 for an excellent review). Suddendorf and Corballis (1997) propose a specific reason for this failure of planning in the so-called Bischof-Köhler hypothesis, which is based on the writings of Wolfgang Köhler (1925), Norbert Bischof (1978), and Doris Bischof-Köhler (1985). This hypothesis posits that the behavior of nonhuman animals is controlled only by current motivational states, and therefore nonhumans cannot anticipate future motivational states (Suddendorf and Corballis, 1997). Although animals do build nests, store food, and move toward the equator for the winter, there is little reason to believe that these behaviors result from anticipation of the future states of parenthood, hunger, or cold. According to the Bischof-Köhler hypothesis, a sated animal cannot anticipate future hunger and act to avoid it, nor can an animal that is not thirsty activate an expectation of future thirst and act to avoid it. If animals are stuck in time as this hypothesis suggests, it represents a major cognitive gap between humans and other animals.

There have been several recent reports of birds and primates apparently planning for the future. Hungry scrub jays (*Aphelocoma californica*) were placed in one of two compartments in alternation over six mornings and allowed to eat the food they found. One compartment contained only kibble and the other only peanuts. The birds were then given both kibble and peanuts for 30 minutes one evening and allowed to cache either food type in the two compartments. The jays cached significantly more kibble than peanuts in the "peanuts

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compartment" and more peanuts than kibble in the "kibble compartment." This ability to distribute food caches in this way suggests that the birds were able to anticipate which food would be available in each room and act to diversify their food selection for the next day (Raby, et al., 2007).

Squirrel monkeys (*Saimiri sciureus*) were reported to act to optimize future rewards, even when it meant forgoing an immediate reward. When presented with a choice between a small and large amount of food, they will normally select the large amount. However, monkeys reversed this preference when presented with a choice between a large amount of food and a small amount of food that was replenished with a large amount 15 minutes later (McKenzie, et al., 2004). Thus, the behavior of the squirrel monkeys was apparently controlled by the occurrence of a food reward 15 minutes after choice, suggesting that they anticipated additional food would follow choice of the smaller amount.

Apes may save tools in anticipation of future need (Mulcahy and Call, 2006). Orangutans and bonobos were trained to use a tool to obtain a food reward from a device. They were then placed in a room where the device was visible but access to it was blocked by a plexiglass shield. This room also contained tools that were within reach, some of which were suitable for use with the device and some of which were not. The apes were allowed to take these tools with them into a waiting room, where they passed one hour before gaining access to the device. On almost half of the trials, apes returned to the room that contained the device carrying a tool that allowed them to obtain a reward. Additional experiments suggested that apes behaved this way even when they had to wait 14 hours to gain access to the device, as well as when the device was not visible when they selected the tool.

Overall, this research suggests that apes, scrub jays, and squirrel monkeys may be able to plan and act to bring about a delayed positive outcome. However, the critical component of the Bischof-Köhler hypothesis that is arguably not addressed by these studies is the stipulation that "true planning" requires anticipation of motivational states that are not currently experienced. Although the jays, squirrel monkeys, and apes altered their current behavior in favor of an outcome that was not immediate, the animals may have been in a motivational state relevant to the goal during the choice phase of the trials (Suddendorf, 2006; Suddendorf and Corballis, 2007, 2008). According to the Bischof-Köhler hypothesis, the remarkable thing about humans stockpiling firewood during the summer months is that this behavior is motivated by the anticipation of being cold, not by the experience of currently being cold. Suddendorf and Corballis (2008) have argued that the squirrel monkeys and apes in the experiments described above may have been motivated to consume the rewards offered during the choice phase of the trials and were therefore acting on current rather than anticipated motivation. They have also argued that the success of scrub jays in planning tasks may depend on a species-specific motivation to diversify food availability. Thus, these experiments may not explicitly address whether the animals made choices in anticipation of a motivational state not currently experienced.

Direct tests of the Bischof-Köhler hypothesis require experimental procedures that ensure that subjects are in different motivational states at the time they perform the target behavior than at the time when the consequences of that action are realized. Two recently completed studies dissociated current and future motivational states and the authors found that nonhuman animals can sometimes anticipate future motivational states and act to alleviate them (Correia, et al., 2007; Naqshbandi and Roberts, 2006).

Correia, Dickinson, and Clayton (2007) used specific satiety to alter jays motivational states and test their ability to plan for the future. All jays were fed kibble and then given the opportunity to cache kibble and pine seeds that they could recover three hours later. Because

they had just eaten kibble, the birds had a preference for eating and caching pine seeds during the caching phase of the trials. However, shortly before recovery of the cached food, birds were fed pine seeds, which led to a preference for eating kibble at recovery. To satisfy their food preference at recovery, birds would need to cache kibble, even though this contradicted the preference for eating pine seeds they had during the caching phase. The birds initially preferred to cache pine seeds, but after only one trial of experience with satiation on pine nuts before cache recovery, they reversed this preference and began to cache kibble almost exclusively. This suggests that scrub-jays were able to anticipate a future motivational state that differed from the current state and were able to act in accordance with the future motivational state.

The Bischof-Köhler hypothesis has also been tested in squirrel monkeys (Naqshbandi and Roberts, 2006). Monkeys were given a choice between a small and large amount of dates in a baseline phase and chose the large amount on the majority of trials. Water access was then made contingent on choice of food quantity. Choice of the larger amount of food was followed by 180 minutes without water, whereas selection of the smaller amount was followed by just 30 minutes without water. The animals had access to water until immediately before the choice phase of each trial and were therefore not thirsty when they chose between the two amounts of food. Naqshbandi and Roberts reasoned that if the monkeys were able to anticipate the 180 minutes of thirst assigned to selecting the large amount of food, they should reverse their baseline preference and instead select the smaller amount, which was assigned to a comparatively short 30 minutes without water.

The squirrel monkeys did learn to select the small amount of food significantly more than the large amount when the water contingencies were in place, suggesting that they anticipated the future motivational state of thirst and changed their current behavior to reduce it. To assess whether or not the monkeys' behavior was controlled by a food aversion induced by the thirst that followed selection of the large amount of dates, the authors gave one of the monkeys an additional free-choice period where no water contingencies were assigned to the food quantities. Preference reversed back to the large amount of food within five trials. The speed of the reversal suggests that the monkey had not learned an aversion to the large quantity, which would be expected to extinguish more gradually, but instead had responded in anticipation of future thirst which no longer occurred. By contrast, rats tested using a similar procedure failed to alter their choice to avoid future thirst and continued to select the large amount of food, suggesting that their choices were governed by the amounts of food, not by anticipation of future thirst (Naqshbandi and Roberts, 2006).

In the present studies we assess whether representatives of an Old World primate species, rhesus macaques (*Macaca mulatta),* anticipate future thirst as was reported for the New World monkeys studied by Naqshbandi and Roberts. Because these two primate species have evolved independently for as long as 42 million years (Steiper and Young, 2006), presence of the ability to plan for the future in rhesus monkeys and squirrel monkeys would suggest that this capacity evolved at least 42 million years ago in an ancestor shared by humans, Old World, and New World monkeys. Rhesus monkeys that were not thirsty were presented with a choice between two amounts of food. Selection of the preferred large amount was followed by a long interval without water, whereas selection of the less desirable small amount of food was followed by a short interval without water. We hypothesized that rhesus monkeys, like the two squirrel monkeys tested by Naqshbandi and Roberts, would learn to select the smaller amount of food, thereby alleviating future thirst. This result would suggest that they can plan for future motivational states and would provide additional evidence against the Bischof-Köhler hypothesis.

The first in the series of experiments that follows used procedures closely modeled after those used by Naqshbandi and Roberts (2006). We then systematically manipulated features of the

experimental design that might inhibit or enhance the expression of planning to better characterize the conditions under which anticipation of future motivational states might occur.

Materials and methods

Subjects

Six male rhesus macaque monkeys (*Macaca mulatta*), aged 3–4 years at the start of the experiment, were kept on a 12:12 light:dark cycle with light onset at 7:00 am. Monkeys were pair-housed in adjoining cages and had full access to their partner at all times expect during testing. Food and water were available ad libitum except as described for each experiment.

Apparatus

Monkeys were tested in their home cage. A separation panel could be inserted between the two monkeys in a pair. This panel confined each individual to a single cage, but had large holes in it that allowed for social contact. A visual barrier could also be inserted between the monkeys to prevent them from viewing tests conducted in the adjacent cage. This barrier completely blocked the opening between the cages and extended 46 cm in front of the cage. Water was available through a spigot at the back of each cage. Access to water could be controlled individually for each monkey by locking a capped PVC pipe over the water spigot in a particular cage. Testing was conducted using a handheld plastic tray (30×56 cm) with two food wells, one on the left and one on the right. Each well was covered by a plastic cup that the monkeys displaced to obtain food. The experimenter wore a darkly tinted face shield during testing to prevent monkeys from seeing the experimenter's gaze.

General Procedure

Prior to the commencement of testing each day, separation panels were inserted between each pair of monkeys to confine them to their own cage. Before each pair of monkeys was tested the visual barrier was also put in place. Following placement of the visual barrier, monkeys were presented with a choice between two plastic cups covering food rewards. Cup and food locations were determined according to a pseudo-random schedule that counterbalanced location across trials. The experimenter held the tray against the front of the cage so that the two choices were equidistant from the monkey. The monkey was allowed to make one choice, defined as the first cup touched, after which the experimenter turned the tray so only the selected choice was within reach, and the monkey was allowed to retrieve all food in that well. After both monkeys in a given pair had made a choice, the visual barrier was removed. The separation panels remained in place until the conclusion of testing each day. Each monkey received one trial per day. Trials began between 13:30 and 14:30 and were conducted six days per week.

Choice Behavior

Proportion correct was calculated in blocks of five trials. Proportions were arcsine transformed prior to analysis to better conform with parametric assumptions (Keppel and Wickens, 2004, p. 155). One-sample t-tests were used to determine whether performance differed from chance in the first and last block of trials in each experiment.

Water Consumption

Thirst is an important variable in the experiments reported. We therefore measured water consumption from a graduated water bottle after the various periods of water restriction used in the experiments (0, 15, 120, and 180 minutes). These water consumption trials were conducted just as regular test trials except that monkeys did not have to choose between cups and were simply fed five half dates from the center of the tray. Once the appropriate interval had elapsed after eating the dates, water was returned in a graduated water bottle. Water levels

were recorded initially and after ten minutes. Finally, the bottles were removed and the monkeys' water spigots were uncovered. Water consumption was measured in this way on three separate trials for each water restriction interval and the three measures were averaged to estimate consumption for each subject at each delay interval. Because mean consumption and variance were correlated, the scores were log transformed prior to analysis to equalize the variance (Keppel and Wickens, 2004, p. 153). Paired t-tests comparing the relevant water consumption for each experiment are reported with that experiment, however, the water consumption data were not collected at the same time the experiments were run.

All statistical tests were two-tailed and used an alpha level of .05.

Experiment 1

Experiment 1 was closely modeled after Naqshbandi and Roberts (2006). Monkeys were given a choice between a large amount of food, selection of which was followed by a long delay before water was returned, and a small amount of food, selection of which was followed by a short delay before water was returned. If choice behavior is controlled by food amount, monkeys should select the cup assigned to the large amount of food and long water delay. However if they can plan for a future motivational state, monkeys should act to avoid future thirst by selecting the cup assigned to the small amount of food and the short water delay.

Procedure

Baseline trials—We assessed initial preference for the two quantities of dates during 20 baseline trials. Monkeys chose between one and four half dates covered by clear plastic cups and were allowed to consume the food selected.

Familiarization trials—Four trials were conducted to familiarize the monkeys with the water contingencies assigned to choice of each amount of food. At the beginning of each trial, the PVC pipe was placed on the water spigot in the monkey's cage, blocking access to water. Monkeys were then presented with the two amounts of food as in the baseline trials, but one cup was secured to the test tray with transparent tape and could not be displaced. Monkeys were thereby required to select the small and large amount of food on two trials each. The order of presentation of these trials and the location of the foods were counterbalanced across the four familiarization trials. Following selection of the small amount of food, access to water was withheld for 15 minutes. Following selection of the large amount of food, access to water was withheld for 120 minutes.

Test trials—Monkeys received 25 experimental trials during which they could choose either quantity of food with the same water contingencies in effect as during familiarization (Figure 1). If at any time during testing a monkey selected the cup assigned to a particular water contingency on five consecutive trials, test trials were stopped and one familiarization trial was conducted before testing was resumed. These trials were run in the same way as the initial familiarization trials, with the cup that had been repeatedly selected secured with clear tape so that the monkey was required to select the alternative cup. This ensured that the monkeys continued to have experience with the two water contingencies throughout testing. Additionally, if at any time during testing a monkey selected the cup located on a particular side of the tray (left or right) for five consecutive trials, test trials were stopped and two familiarization trials were conducted before test trials resumed. These two trials were run in the same way as the initial familiarization trials. Only the neglected side (left or right) was available on these trials, and one trial was conducted for each of the two water delay contingencies. This prevented monkeys from developing side biases.

Results and Discussion

The long 120 minute period without water induced significantly more thirst than the short 15 minute period, as demonstrated by a significant difference in water consumption after the two intervals (15 Minutes: M=40.83 mL; 120 Minutes: M= 51.17 mL; $t(5)$= −4.04, p=.01).

Monkeys selected the large amount of food on baseline trials and continued to show this preference over the 25 experimental trials, despite the greater thirst induced by the long interval without water that followed selection of the large amount. Choice of the large amount of food was significantly above the level expected by chance on both the first and last blocks of baseline trials (First Block: $t(5)$=4.41, p= .01; Last Block: $t(5)$=9.26, p= .01; Figure 2, left panel). Similarly, choice of the large amount of food was significantly above the level expected by chance on both the first and last blocks of experimental trials (First Block: M=1.0, SEM=0, no test conducted; Last Block: $t(5)$= 9.26, p<.01; Figure 2, right panel). The monkeys established a preference for the large amount of food on baseline trials and this preference continued despite the addition of the water contingencies in the experimental trials.

Like the squirrel monkeys in Naqshbandi and Roberts (2006), the rhesus monkeys clearly preferred the large amount of food in baseline trials. Unlike the squirrel monkeys, the rhesus monkeys did not change their preference on experimental trials where selection of the large amount of food resulted in greater thirst later. These results differ from those reported by Naqshbandi and Roberts and do not support the hypothesis that rhesus monkeys can anticipate motivational states.

Experiment 2

In Experiment 1 monkeys may have been unable to inhibit the prepotent tendency to select a visible large amount of food. Previous research has demonstrated that chimpanzees are better able to inhibit their tendency to select a large amount of food when the food is replaced with associated tokens (Boysen, et al., 1999). In Experiment 2 we used the same procedure as used in Experiment 1 except that the dates were covered by two distinct opaque cups. Blocking visual access to the food may curb the tendency to select the large amount of food and make it more likely that the monkeys' choice behavior is controlled by the water contingency. If monkeys were able to anticipate future thirst in Experiment 1 but could not express this knowledge because they could not inhibit choice of the visible large quantity of food, then covering the foods should facilitate performance.

Procedure

Water contingencies and amounts of food remained the same as in Experiment 1, but the two plastic cups were now opaque and distinctive. One was covered in black electrical tape and the other in white electrical tape. Assignment of cup designs to delay length was counter balanced across subjects. No baseline trials were run in this or any subsequent experiments, as we had already established the strong preference for the large amount of food. All other procedures were the same as in Experiment 1 except that testing concluded when a monkey completed at least 20 trials and selected the same cup on 5 out of 6 consecutive trials.

Results and Discussion

Because the monkeys did not know initially which amount of food and which water contingency was assigned to each cup, selection of the cups should start at chance and change as monkeys learn the contingencies assigned to each. Monkeys did initially chose the two cups equally, but learned to select the cup assigned to the large amount of food and long delay significantly more than expected by chance by the last block of five trials (First Block: $t(5)$= 1.56, p= 0.18; Last Block: $t(5)$= 6.53, p<.01; Figure 3). Despite the increased thirst induced by

the long delay, choice behavior was again controlled by amount of food rather than delay to water access. The failure of monkeys to demonstrate sensitivity to the water contingencies in Experiment 1 was not due to an inability to inhibit selection of a visibly larger amount of food. As in Experiment 1, these results do not support the hypothesis that monkeys can alter current behavior to alleviate a future motivational state.

Experiment 3

In Experiments 1 and 2, monkeys showed no evidence that they anticipated future thirst. However, it is possible that monkeys are able to anticipate future motivational states, but did not express this ability under the test conditions. In Experiment 3 we address three methodological reasons that monkeys may have been unable to learn to avoid the long interval without water in Experiments 1 and 2. First, the monkeys may have been unable to inhibit their tendency to select the large amount of food even when the food was concealed under an opaque cup. Second, monkeys may have continued to select the large amount of food because the subjective value of the large food reward outweighed the subjective cost of future thirst. Third, the monkeys may have difficulty discriminating the 15 minute delay from the 120 minute delay because the amounts of thirst assigned to these two intervals may have been too similar, despite inducing significantly different amounts of drinking. We addressed the first and second concerns by using equal amounts of food for both choices and the third concern by extending the long interval without water from 120 to 180 minutes. In the present experiment, monkeys should therefore be better able to learn to choose the cup assigned to the short water delay because the difference between the delays has been made more salient and is now the only relevant contingency.

Procedure

Two new distinct opaque cups were used; each concealed five half dates. The short water delay remained 15 minutes, but the long delay was increased to 180 minutes. Testing concluded when a monkey either completed at least 25 trials and selected the cup assigned to the short delay on 8 out of 10 consecutive trials, or when the monkey completed 35 trials. The experiment was otherwise run exactly as Experiments 1 and 2.

Results and Discussion

The long 180 minute delay induced more thirst than the short 15 minute delay, as indicated by the difference in water consumption between these two periods (15 Minutes: M= 40.83 mL; 180 Minutes: M= 52.67 mL; $t(5)$= −2.88, p=.03). Although the long delay induced significantly more thirst than the short delay, selection of the two cups did not differ from chance in either the first or last trial block (First Block: $t(5)$= −0.80, p=.46; Last Block: $t(5)$= − 1.39, p=.22; Figure 4). Monkeys showed no preference for either cup when the amounts of food were equal, suggesting that they were insensitive to the two water contingencies despite the significantly greater thirst induced by the long delay. Failure to learn in Experiments 1 and 2 was not due to an inability to inhibit choosing the large amount of food. As in Experiments 1 and 2, the monkeys' performance in this experiment provides no evidence that they anticipate future motivational states.

Experiment 4

According to the logic of the Bischof-Köhler hypothesis, monkeys needed to do two things to succeed in the previous three experiments. First, they had to anticipate that they would be in a motivational state in the near future that differed from the state they were in when making their choice. Second, they had to know which cup was assigned to the outcome that would alleviate this future motivational state. Failure of either of these components would result in failure on

the task, but importantly, only the motivational component is directly relevant to the Bischof-Köhler hypothesis. Humans who stockpile firewood in the summer do so because they anticipate being cold in the coming winter. However, this ability to act to alleviate future cold relies on the knowledge that firewood is used to make fire which wards off cold. Without knowledge of the function of firewood, even a human anticipating future cold would not stockpile firewood. If the monkeys in the present study could not associate a particular cup with water return, then they could not possibly plan adaptively, even if they could anticipate that they would be thirsty in the future.

In Experiments 1–3 monkeys may have been unable to learn the contingency between the cups and the water delays because the water was returned long after selection of a cup, 15 minutes in the case of the shortest delay. Expression of most operant learning is optimal when the reinforcing outcome follows the target behavior immediately, and declines rapidly as the delay to the outcome increases (Roberts, 2002). It is also possible that the water contingencies we have used were not sufficiently motivating for rhesus monkeys to support learning under any conditions. In Experiment 4, we tested whether the contingencies we have used are sufficient to support learning under ideal conditions by returning water immediately after selection of a cup. If monkeys learn to select the cup assigned to the short water delay under these conditions, it would suggest that the stimuli used in the experiments were sufficiently motivating to support learning but that the monkeys could not learn associations at a 15 minute delay. Because monkeys would still be in a different motivational state during choice than when water was returned, success in this experiment would suggest that the failure to learn in Experiments 1–3 was due to an inability to learn associations between the cups and the return of water more than a minute in the future, rather than due to a failure to anticipate a motivational state not currently experienced.

Procedure

All procedures were the same as in Experiment 3 with two exceptions. First, new distinct cups concealed the dates. Second, the short water delay was decreased from 15 to zero minutes. The zero minute delay meant that access to water was restored as quickly as possible after selection of the short delay cup (approximately 40 seconds). Testing concluded when a monkey completed at least 15 trials and had selected the cup assigned to the short delay on 8 out of 10 consecutive trials, or when the monkey had completed 35 trials.

Results and Discussion

The zero and 180 minute delays did not induce different amounts of drinking (Zero Minutes: M=80.71 mL; 180 Minutes: M=52.67 mL; $t(5)$=0.57, p=.59). Somewhat surprisingly, monkeys drank significantly more water after the zero minute delay than after the 15 minute delay (Zero Minutes: M=80.71 mL; Fifteen Minutes: M=40.83 mL; $t(5)$=2.62, p=.05). The large amount of drinking evident at the zero minute delay presumably reflects a motivation to drink immediately after eating dates that attenuates shortly after the dates are swallowed and the mouth is cleared of food.

Monkeys did learn to select the cup assigned to the short delay when the delay was decreased to zero minutes, whereas they had not learned in the previous three experiments (First Block: $t(5)$= −4.19, p=.01; Last Block: $t(5)$= −4.22, p= .01; Figure 5). The significant preference in the first block of trials suggests that monkeys learned this association rapidly during the initial four familiarization trials. The ability to rapidly learn to select the short delay in this experiment demonstrates that the failures to learn in Experiments 1–3 were not due to an inability to learn an association between a cup and a water delay under any conditions, but were instead a function of the long interval between choice and access to water. Most important with respect to the Bischof-Köhler hypothesis, monkeys were not thirsty when they made their choice, but

selected the cup that would decrease the thirst they would experience after choice. Despite the short interval between choice and the return of water, this demonstrates that monkeys can anticipate a motivational state they do not currently experience and act to alleviate it. As there has been no specification of how much time must elapse before a motivational state qualifies as occurring in "the future", the results of Experiment 4 technically contradict the Bischof-Köhler hypothesis.

Experiment 5

In Experiment 4 the monkeys did select the cup assigned to the immediate return of water despite not being thirsty at the time of choice. This result suggests that the main impediment to planning by our monkeys in Experiments 1–3 may not have been the inability to anticipate future motivational states, but instead was difficulty learning to associate the cups with the return of water across a long delay. To further assess the relative importance of motivational states and choice-outcome delays, we ran a final experiment in which we again used 15 minutes for the short delay to water return as in Experiments 1–3, but ensured that monkeys were in the same motivational state at choice as when they experienced the outcome of the choice. Thus there was no requirement to anticipate a motivational state not currently experienced. The monkeys had only to learn to associate their choice of cup with the return of water 15 or 180 minutes later. This final experiment also address the possibility that the difference in performance between Experiments 3 and 4 was due to a difference in the subjective value of water return in these two experiments. We observed that the monkeys drank more water immediately after eating dates than they did 15 minutes after eating dates, indicating that the return of water after the short delay used in Experiment 4 may have been more reinforcing than it was in Experiment 3. If this were the case, then feeding the monkeys additional dates immediately before the return of water at the 15 minute delay would make the water as rewarding as it was after the zero minute delay and allow the monkeys to develop a preference for the short delay.

In Experiment 5, we prefed the monkeys dates immediately before the initial choice between the two cups, ensuring that monkeys were in the same motivational state of thirst at the time of choice and water return outcome. We also gave monkeys additional dates prior to water return at 15 minutes, ensuring that the water return after 15 minutes was as rewarding as it was after zero minutes in Experiment 4. If the failure to perform in Experiments 1–3 was due to a failure to anticipate future motivational states or to the low reinforcement value of water return after the 15 minute delay, monkeys should learn to select the short 15 minute delay cup in this experiment. In contrast, if the reason for their poor performance on Experiments 1–3 was difficulty learning associations between cup choices and outcomes at a long delay, they should show no preference for either cup, as in Experiment 3.

Procedure

The procedure of Experiment 5 differs from that of Experiments 1–4 (Figure 6). Prior to the choice phase, subjects were fed 5 half dates placed on the center of the test tray, to increase their motivation to drink. Because monkeys ate dates immediately before choice, small chocolate pieces were concealed under the distinct opaque cups at choice to motivate them to select a cup. Assignment of the new distinct opaque cups to either the short delay of 15 minutes or the long delay of 180 minutes was counterbalanced across monkeys.

Fifteen minutes after the choice phase of each trial monkeys were given an additional five half dates, regardless of which cup they chose. On trials where they selected the short delay cup, water was returned immediately after they were fed these additional dates. On trials where they selected the cup assigned to the long delay, water was returned 165 minutes later (a total of 180 minutes after the choice phase). Testing concluded when a monkey completed at least 15

trials and selected the cup assigned to the short delay on 8 out of 10 consecutive trials or completed 35 trials.

Results and Discussion

Monkeys did not show a preference for the short delay cup in either the first or last block of trials (First Block: $t(5)= -0.58$, $p=.59$; Last Block: $t(5)= -0.94$, $p=.39$; Figure 7). Even when the procedure ensured that monkeys were thirsty during the choice phase and that the return of water would be highly rewarding, monkeys apparently did not learn to associate the cups with different delays to the return of water. Therefore, the difference in performance in Experiments 3 and 4 is most likely due to the difference in the interval between the choice phase and the return of water. Monkeys did learn in Experiment 4 when the delay between cup choice and water return was minimal, but not when this delay was 15 minutes long in Experiments 3 and 5. This pattern of performance is consistent with traditional accounts of learning that emphasize temporal contiguity.

Discussion

Together, the results from the five experiments reported suggest that rhesus monkeys were unable to act in anticipation of motivational states that occurred as little as 15 minutes in the future. The monkeys did not learn to avoid future thirst in Experiments 1, 2, 3, and 5 even though the stimuli used in these experiments were shown to be sufficient to support learning at a short delay in Experiment 4. Monkeys did anticipate a motivational state not currently experienced in Experiment 4 when the delay between choice and outcome was short. The ability of our monkeys to anticipate a future motivational state, albeit one that occurred in the very near future, suggests that the monkeys' failure to display planning in the other four experiments was likely due to difficulties learning the necessary contingencies, and not to a failure of planning in the Bischof-Köhler sense. These results are consistent with traditional accounts of operant learning that emphasize the importance of temporal contiguity between behavior and reinforcers (Roberts, 2002; Shettleworth, 1998, p.119). In the discussion below, we first comment on the relationship between our findings and those of Naqshbhandi and Roberts (2006), and then address more general issues about planning and the Bischof-Köhler hypothesis.

Our methods were closely modeled after those used by Naqshbandi and Roberts (2006), but our negative results from Experiments 1, 2, 3, and 5 contrast with their report that squirrel monkeys altered their preference for a large amount of food to avoid future thirst. There are many possible reasons for not finding the same effect in rhesus monkeys that Naqshbandi and Roberts found in squirrel monkeys, and the present negative results cannot be taken as proof of the absence of the capacity for planning in rhesus monkeys. The squirrel monkeys in Naqshbandi and Roberts (2006) study were apparently able to learn associations between their behavior during the choice phase of trials and the return of water 30 or more minutes later, while our rhesus monkeys were not. However, the monkeys in Naqshbandi and Roberts' study had more than a decade of previous experience with a variety of cognitive tests including tests in which they had learned to inhibit immediate preferences to maximize long-term rewards (McKenzie et al., 2004; W.A. Roberts, personal communication, September 7, 2007). It may be that these subjects were prepared by this experience to quickly learn to associate their behavior with delayed outcomes. If our rhesus monkeys had a similar long history of training it is possible that they would have learned as well.

Alternatively, cognitive, motivational, or other differences between squirrel monkeys and rhesus monkeys might account for the fact that we did not obtain results similar to those of Naqshbandi and Roberts (2006). It is possible that some yet to be identified difference in life histories may account for the independent evolution of planning in squirrel monkeys but not

rhesus monkeys. Because humans are the only species known with certainty to have the capacity to plan, the occurrence of planning in squirrel monkeys but not our closer rhesus macaque relatives would otherwise represent an unparsimonious phylogeny of planning. It may be more likely that differences in the ecology of the two species have led to motivational differences that affect performance on these specific planning tasks. Squirrel monkeys live in rainforests and consume a moisture-rich diet of fruits and insects (Jack, 2007). They may have a lower tolerance for restricted water access than do rhesus monkeys, which live in a variety of habitats including some that are quite arid (Thierry, 2007). It is therefore possible that rhesus monkeys had more difficulty with the current test than squirrel monkeys because of a species difference in the subjective value of access to water. Thus, rhesus monkeys might be equally capable of planning for the future but did not express this capacity under the current conditions. This explanation seems unlikely, however, because the long delays used in Experiments 1, 2, 3, and 5 did induce significantly more thirst than did the short delays. If they could anticipate future thirst, monkeys should have learned to select the cup assigned to the shorter water delay in these experiments, but they did not. Comparable water consumption data for the squirrel monkeys that would allow for a direct comparison is not available.

Through systematic manipulation of aspects of Naqshbhandi and Roberts (2006) original experimental design, we were able to assess the ability of monkeys to anticipate future motivational states separately from their ability to form associations across long delay intervals. When the short delay to the return of water was decreased to zero minutes in Experiment 4, the monkeys learned to select the cup assigned to this short delay. The results of Experiment 4 demonstrate two things: 1) the monkeys could learn associations between the cups and the return of water when the interval between choice and outcome was brief, and 2) the monkeys could learn to select the cup assigned to the short delay to water even when they were not thirsty at the time of choice. Apparently, it was the length of the delay between selection of a cup and restoration of access to water that prevented learning, as the other features of these experiments were sufficient to support learning. Even in Experiment 5, which was designed to give monkeys the best chance to respond to the water contingencies in the face of the long choice-outcome interval, the monkeys still failed to learn. Neither increasing the reward value of water by feeding the monkeys extra dates immediately before water was returned, nor eliminating the need to anticipate future thirst by inducing thirst before choice, helped the monkeys associate choice behavior with later access to water.

Because we have ruled out other likely explanations for the failure to learn, the results appear consistent with classical principles of associative learning that emphasize temporal contiguity. The short delay between choice and water return in Experiment 4 likely facilitated learning of the cup-outcome associations. Because the monkeys were not thirsty when they made their choice in Experiment 4, they technically acted to alleviate a future drive state, contradicting the Bischof-Kholer hypothesis. Combined with the negative results of Experiment 5, in which we ensured that the monkeys were in the same motivational state at choice and outcome, our results suggest that difficulty anticipating future motivational states may not be the limiting factor in nonhuman planning in this task. The lack of planning displayed in Experiments 1, 2, 3 and 5 was probably due to an inability to learn associations between the cups and the associated water outcomes at long delays, rather than to an inability to anticipate future motivational states.

As stated above, monkeys needed to know which cup was assigned to which water return outcome in order to show evidence of planning in these experiments. This knowledge could only be acquired from experience in the familiarization or test trials. It is well established that under most conditions, the expression of learning is strongest when the timing between the relevant events is short, generally between 0–30 seconds (Roberts, 2002; Shettleworth, 1998, p.120). Even in flavor aversion learning, which peaks at comparatively long delay intervals,

performance declines as the interval increases beyond one hour (Barker and Smith, 1974). The delays between cup choice and the return of water in the present experiments were 15, 120, and 180 minutes, which are all longer than those typical of successful associative learning. Because associative learning mechanisms are generally not effective at these long delays, it is likely that monkeys failed to associate the cups with the two water delay outcomes in all experiments except Experiment 4. If monkeys did not learn the associations between the cups and the different delays to water return, they could not express planning even if they could anticipate a future motivational state.

In distinguishing human planning from various performances by nonhumans, Suddendorf and Busby (2005) have argued that demonstrations of true planning must rule out other possible explanations, such as associative learning and instinctive behaviors. To exclude these possibilities, they make two suggestions. First, tests of planning should prevent trial and error learning, which could lead to the gradual acquisition of behavior-outcome associations. Second, they argue that tests of planning should not use species typical behaviors, which might give the impression of planning, but may actually depend on specialized long delay associative learning mechanisms akin to flavor aversion learning (Busby and Suddendorf, 2005; Suddendorf and Corballis, 2008). Arguably, none of the existing evidence for planning in nonhuman animals fully meets these criteria (Shettleworth, 2007; Suddendorf and Corballis, 2008). Studies in scrub jays are limited to food caching (Correia, et al., 2007; Raby, et al., 2007), which is a specialized species typical behavior (Shettleworth, 2007), and studies in monkeys (Naqshbandi and Roberts, 2006) have been criticized because they may have allowed sufficient experience for trial and error learning to be effective (Shettleworth, 2007; Suddendorf and Corballis, 2008). The experiments described in this paper and those conducted by Naqshbandi and Roberts (2006) were not designed to rule out trial and error learning.

It is not clear whether the additional criteria described above are necessary or sufficient for demonstrations of planning, or even whether they accurately characterize planning in humans. For example, ruling out trial and error learning may be impossible in most tests of planning. As stated above, if subjects have not had the necessary experience to acquire knowledge of the contingencies relevant to a given task, then apparent failures of planning may simply reflect lack of the relevant knowledge. Even most human planning likely violates this "limited experience" criterion, as humans have countless experiences with the outcomes of behavior, making it almost impossible to separate instances of true planning from those based on repeated past experiences or generalization from related trial and error learning. Disregarding planning that occurs in the context of species typical behavior also seems unjustified. If rapid, flexible learning can be shown within species specific domains, as with food caching in scrub jays (Clayton, et al., 2003; Correia, et al., 2007; Dally, et al., 2006; Raby, et al., 2007), it seems unlikely that the planning behavior displayed is the result of "instinct", as Suddendorf and Busby (2005) suggest. Finally, realistic criteria for planning in nonhumans should reflect the fact that humans often have great difficulty planning adaptively, as evidenced by the large number of people who smoke or fail to save for retirement. Understanding the factors that facilitate and impair the capacity to plan in humans may aid in designing better experiments to test for planning in nonhumans. We anticipate that the Bischof-Köhler hypothesis and other conceptualizations of planning will evolve in response to new empirical results and as the mechanisms underlying planning are better specified.

Acknowledgments

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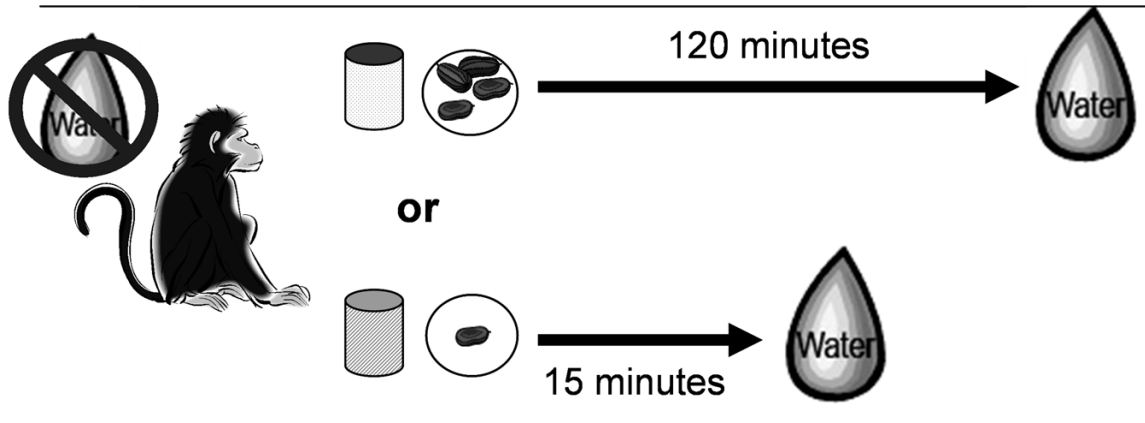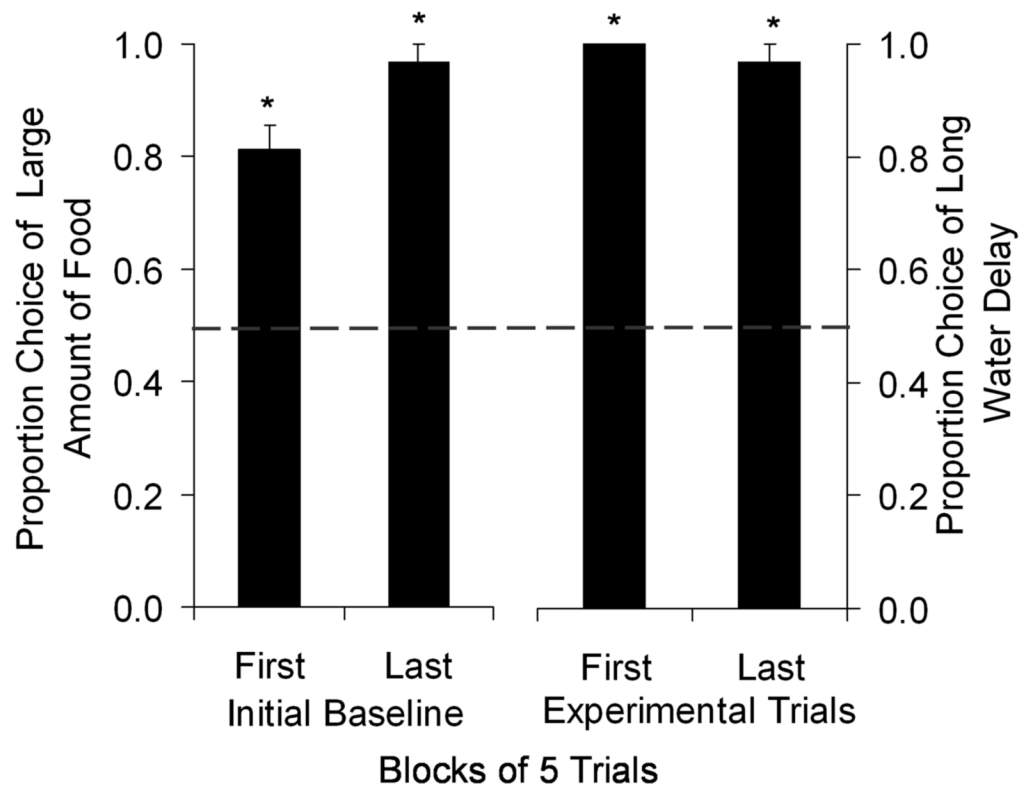
Figure 1.

Figure 2.

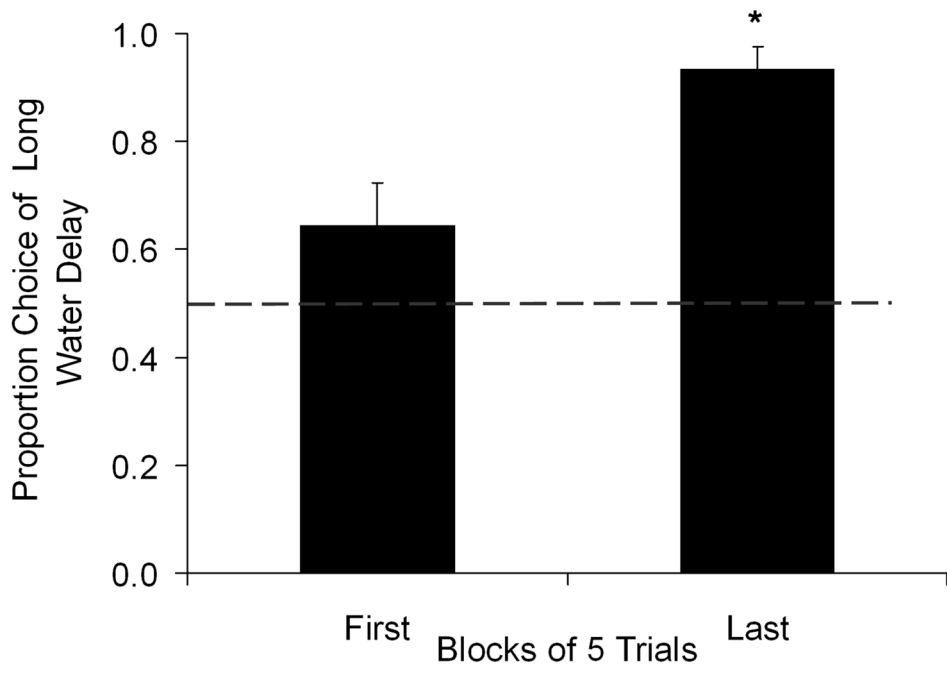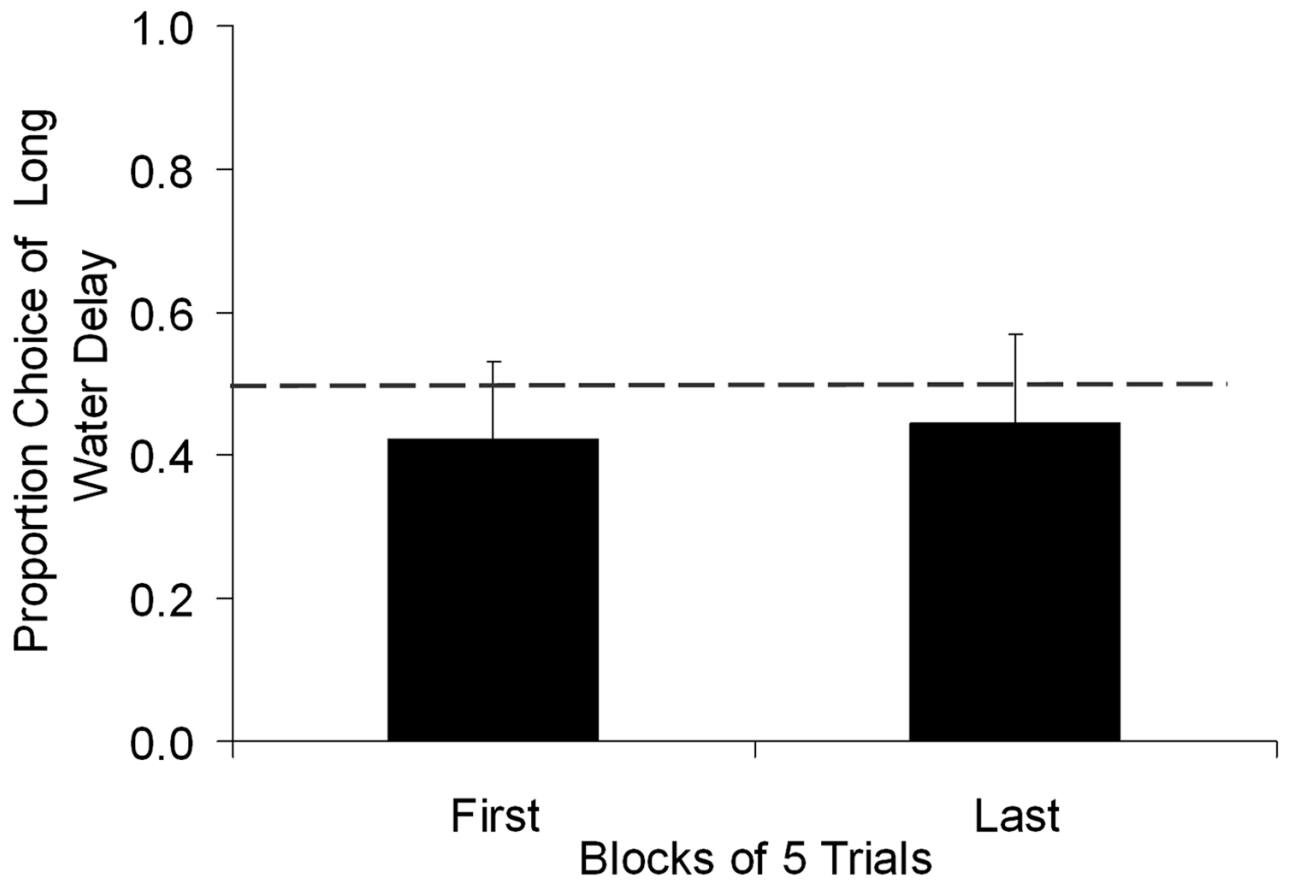**Figure 3.**

Figure 4.
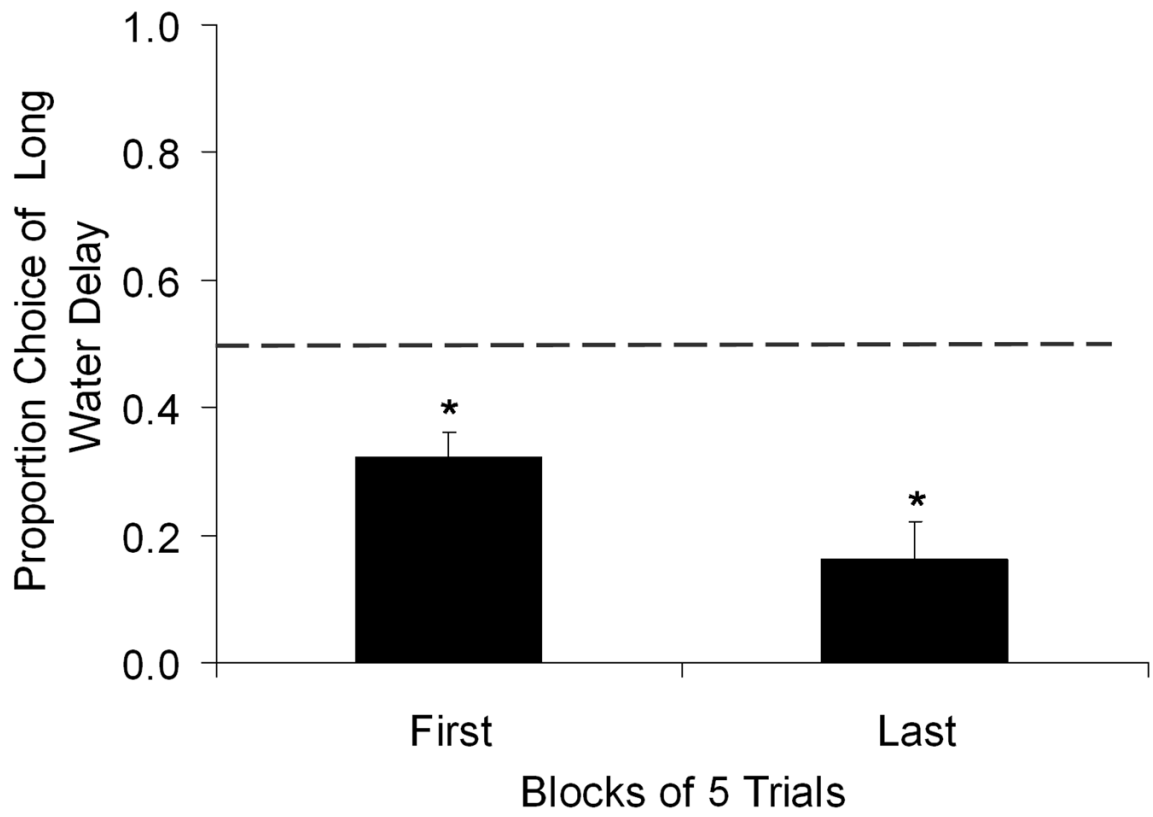
Figure 5.

Figure 6.

Figure 7.