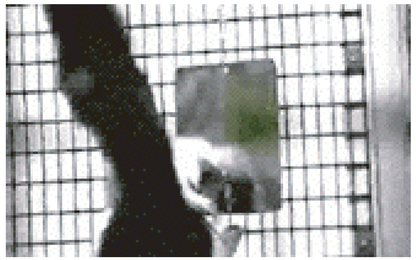

Deciphering the Code: The Relative Influence of Geometric and Nongeometric Cues in Spatial Foraging by Cotton Top Tamarins (*Saguinus oedipus*)

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Abstract

A new method presented geometric and nongeometric cues to cotton top tamarins, and then tested their ability to use each type of cue to find treats separately. Tamarins (n=6) learned to find the site with the heaviest baiting out of 3 possible sites. In tests in which geometric or nongeometric cues were presented alone, tamarins continued to select the site associated with the most food. When both types of cues were pitted against each other in a conflict test, tamarins switched to choosing less often a particular site when the overall value of the two cues combined was weaker. Tamarins' choices confirmed that they integrated the cues, used them in isolation, and assessed their combined values at each site.

Background

When different species of animals are studied while they search for food in particular known baited areas, an important comparative question is what sorts of cues each species can use to re-trace its way to the remembered food sites. The cues most often studied are: 1) geometric cues, or the absolute location at which an item occurs as referenced by spatial representations such as a cognitive map or a navigational system, and 2) nongeometric cues, typically defined as landmarks or visual cues that are memorized and that mark the site to revisit. Recent investigations have tried to tap into the sophistication and flexibility with which different monkey species can represent simultaneously both geometric and nongeometric cues to find food sites (for example, in rhesus monkeys; Gouteux, Thinus-Blanc & Vauclair, 2001; in long-tailed macaques, Menzel, 1996; in tamarins, Deipolyi, Santos & Hauser, 2001).

From the perspective of the classical conditioning of multiple cues, one would expect that monkeys would acquire associations between food and the absolute location of the food, and any relative and visual cues available as well, although the weighting of such cues might be related to predispositions to store spatial information more by visual cues or more by absolute location. In fact, several interesting findings have emerged:

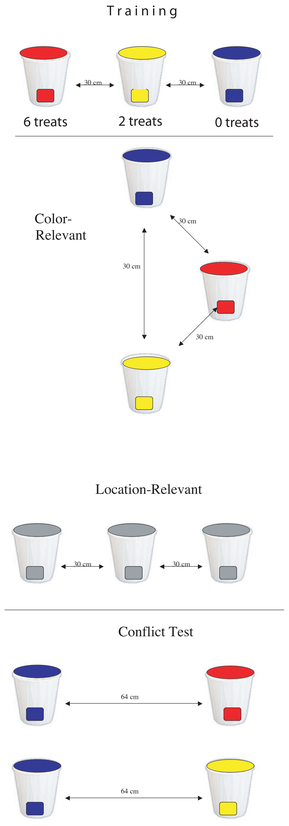
* Rhesus monkeys only make use of visual markers to find food locations when they are of substantial size, and thus may seem more connected to the location itself (or more permanent as nongeometric cues).

* Children do not make use of visual markers to find the relevant location of a toy until a particular age of development, although it is possible that in the studies with children, the visual markers seemed less permanent (children viewed them as they were placed on the wall as a cue, or played with "toy" cues that moved before the toys were used to mark the locations (Hermer & Spelke, 1994)).

* Tamarins seemed predisposed to use visual markers to indicate locations for food, because in contrast to the studies above, they were able to use visual landmarks, even if they were altered by color or shape, but could not reliably find the food locations when the visual landmarks were removed.

The outcomes of these experiments seem at odds with the notion that most primates should be able to code reward associations with multiple cues simultaneously. The method used in all was Cheng's disorientation procedure which puts the subjects in an ambiguous spatial area with two corners which could be confused spatially to be the "correct" corners (one corner and its 180 degree rotational equivalent). The current study used a basic foraging method with three absolute locations (geometric cues) and with relative location (left, middle, and right) and color cues as the nongeometric cues provided. Thegeometric and nongeometric cues were extracted by type (color cues removed, and later, the relative and absolute location cues removed) to test whether the tamarins would reach for food in the spot that should be associated with the highest reward if multiple cues (geometric and nongeometric) had been coded simultaneously and could be used in isolation of the other cues. Finally, color nongeometric cues and location geometric cues were pitted against each other in a conflict test.

Method



The subjects were six adult cotton-top tamarins (Saguinus oedipus) with 2 female (Fozzy and Caitlin) and 4 male subjects (Rolo, Yohoo, Zhivago, and Mac) in the group.

Small white plastic cups, 8 cm tall and 3.5 cm in diameter, were attached in an upright fashion to the inside of the cage by means of a safety pin at a location approximately 1 m above the floor of the cage. Each cup had a small window (2.5 cm square) cut in its side, and a cloth covering both its top and the window opening. Rewards were mini-marshmallows, cut in half. Subjects were first habituated to the cups and trained to reach for rewards in them in a condition in which only 2 cups were present, both with black coverings, and both baited with rewards. When subjects reached in and received 2 rewards from each cup within 2 minutes, the training procedure began.

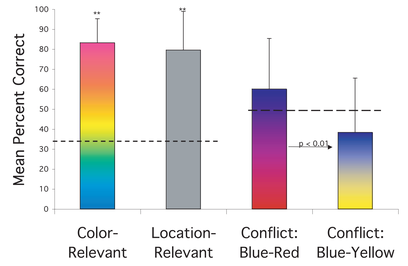
Training sessions consisted of 5 2-minute trials , and in every trial, the three colored cups were baited differentially and presented simultaneously. For each trial, the three cups were placed in a straight row at a height of 1 m above the cage floor and spaced relative to its adjacent cup 30 cm apart. See the Figure to the left for the cups in the TRAINING ARRAY. Once subjects achieved 80% correct selection to Slot 1/red cup first within one session, they were tested, with half receiving color-relevant test first, and half receiving location-relevant test first. All subjects received the conflict test last.

Location-relevant test: In this test, three cups all of a neutral color (gray) were placed at each of the three original training locations (see Figure, left). Two sessions of a total of 10 trials were presented and all cups were baited with 2 treats.

Color-relevant test: The three colored cups were re-located such that no one occupied an absolute location used before, but such that the cups were still similarly equidistant from each other (see Figure, left). Two sessions of a total of 10 trials were presented and all cups were baited with 2 treats.

Conflict tests: Two different test trial types were presented, 5x each, within two test sessions. In both types of trials, only two cups were used, thus chance performance at any one cup raised from 33% to 50%. In one test, the red cup formerly associated with high-reward was placed in the location formerly associated with no-reward; and similarly, the colored cup formerly associated with no reward (blue) was placed in the high-reward location. This conflict puts the nongeometric cue of color directly in conflict with the geometric cue of location. The second test type degraded the associative strength of the color placed at the no-reward location: in this case, the red cup (high reward) was replaced with a yellow cup (middle-value reward), still at the no-reward location. The no-reward colored cup, blue, was placed in the high reward location here as well. (see bottom, Figure to the left for examples).

Results



It took an average of 10.33 sessions (range of 5 – 17 sessions) for subjects to select the Slot-1/red cup first at the level of criterion performance, or 80% correct within one session. Subjects were also required to demonstrate criterion performance between each test condition (color-relevant, location-relevant, and conflict tests), and this took, on average, 1.5 sessions between the first and second tests, and 2.67 sessions between the second and third (conflict) tests.

In the location-relevant condition in which all cups were gray, subjects selected Slot-1 first on average on 79.50% of the 10 trials of testing, and their selection was significantly above chance level, or 33% choice for any one of 3 cups, as determined by a one-sample t-test against a hypothetical mean, $t(5) = 5.89$, $p < 0.01$.

The color-relevant condition provided a red cup in a triangular-shaped array such that it was in a novel location, and subjects selected the red cup first 83.17% of the time, also significantly above chance would predict for that cup, ($t(5) = 10.22$, $p < 0.01$).

There were two conflict conditions in which there is no clear "correct" choice. Subjects' choices were coded in terms of color (wherein "red" and "yellow" would be the correct choices, respectively). Chance level performance was 50% in these tests. Neither condition produced choices significantly above chance (for red, mean = 60.00, $t(5) = 0.97$, $p = 0.37$; for yellow, mean = 38.33%, $t(5) = -1.05$), $p = 0.34$).

Still, the subjects' choices indicated a switch in the process of selecting the blue cup across the two conflict conditions, as demonstrated by a pairwise related samples t-test, $t(5) = 5.40$, $p = 0.003$. Clearly subjects favored the blue cup more in the blue-yellow test than they did in the blue-red test. This demonstrates that when both choices do not pay off well, the tamarins resorted to favoring a no-reward color in a high-reward location to a low-reward color in a no-reward location.

Discussion

This experiment demonstrates that tamarins can use absolute and relative location to forage efficiently for the spot with maximum reward, as shown by their ability to pick Slot 1 (with the correct absolute location, and relative left) when the color cues were removed. Tamarins were also able to instantly select by using color cues, as shown by their preference toward the red cup in the new array when the absolute location and relative positioning were removed. In contrast to the Deipolyi, Santos & Hauser (2001) study, tamarins were immediately successful at finding food when visually distinct landmarks were removed.

In terms of the use of cues with acquired associative strength, it appears from the conflict tests that tamarins combine in an interesting way the relative weights of location and color to select a foraging spot. Specifically, they tended to favor a color which predicted high-reward when both location and color canceled each other out. With two color cues of relative low strength, a bias toward the more salient location emerged.

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