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ORIGINAL ARTICLE

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The role of landmarks in cotton-top tamarin spatial foraging: evidence for geometric and non-geometric features

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Abstract We report experiments on captive cotton-top tamarins (*Saguinus oedipus*) designed to explore two components of spatial foraging. First, do tamarins have the capacity to extract geometric information concerning the spatial relationship between a landmark and a piece of food located above or below it? Second, when tamarins use a landmark to find a target location, what non-geometric features of the landmark do they encode? To explore these problems, we created an artificial jungle environment and trained subjects to find food either above or below a target object (i.e., landmark). Once subjects successfully located the food, we transformed various features associated with the landmark, including its color, orientation, and shape; we also manipulated the landmark-food reward distance, the overall shape of the jungle, and the number and position of landmarks. Results showed that the tamarins' success in finding the food reward was not affected by landmark color, orientation, number, or overall shape of the jungle, suggesting that with respect to the particular test conditions, these features are not relevant to the representation of a landmark. Subjects also generalized to novel landmark-food distances, suggesting that they had integrated geometric (i.e., above/below) with non-geometric (i.e., color/shape) features. Performance was negatively affected by changes to the shape of the landmark, indicating that this feature is critical to the representation of a landmark.

Keywords Spatial foraging · Primates · Geometric features · Landmarks

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Introduction

When visually guided animals navigate through an environment, they can tap both geometric and non-geometric features to return home or find a food source (Cheng 1986; Cheng and Spetch 1998; Etienne et al. 1998; Gallistel 1990; Hauser 2000; Kamil and Jones 1997; Spelke and Tsivkin, in press; Vallortigara et al. 1990). Although there is evidence that some animals can integrate geometric (i.e., metric relations between spatial elements) and non-geometric (i.e., landmarks/beacons) features under certain conditions (Collett et al. 1986; Spetch et al. 1996; Spetch et al. 1997; Gouteux et al., in press), this capacity does not generalize across all spatial tasks and all species. The current study was motivated by two aspects of this problem. First, under what conditions do animals integrate geometric and non-geometric information during a spatial task? Second, when animals attend to non-geometric properties of the environment, such as a landmark, which features are most salient? We address these questions through a series of experiments on cotton-top tamarins, a species for which we know a considerable amount about their problem-solving capacities during non-spatial tasks, but little about their understanding of spatial tasks.

In a disorientation task originally developed by Cheng (1986), and subsequently modified by Hermer and Spelke (1994, 1996), results show that rats and human toddlers fail to integrate geometric with non-geometric information. Specifically, when subjects are placed in a rectangular room with four white walls, shown the corner with a concealed reward, disoriented (i.e., spun around with eyes closed), then allowed to search, they look in either the correct corner or the geometrically opposite one. This shows that both rats and toddlers use the geometry of the room to navigate to a goal. Interestingly, when the color of one wall is changed, providing a non-geometric cue, both rats and toddlers continue to search in both the correct and geometrically opposite corners, showing that they fail to integrate geometric with non-geometric information. Hermer-Vazquez et al. (1999) showed that human adults behave like rats and toddlers in the all-white room condition, but consistently pick the correct corner when one wall has a different color from the other three. Surprisingly, adults perform like rats and toddlers when they attempt the same task while simultaneously engaged in verbal shadowing. Based on this pattern, Hermer-Vazquez and colleagues suggest that in humans, some aspects of language may be necessary to integrate information from two different spatial systems (also see Spelke and Tsivkin, in press).

In contrast to rats and human toddlers, other species, including chickens (Vallortigara et al. 1990), pigeons (Kelly et al. 1998) and rhesus monkeys (Gouteux et al., in press), are able to reorient based on both geometric and non-geometric features of the environment. These results suggest that the integration of information from two different spatial systems may be species-specific. Alternatively, differences in performance may be the result of slight, but important differences in methodologies. An important goal of work in this area, therefore, is to extend the range of species tested, in addition to the range of spatial tasks explored.

The second problem motivating our work was to determine which landmark features are most salient to tamarins in locating a target reward, or what is often referred to as cue control in landmark use (Etienne et al. 1998; Spetch and Edwards 1988). Animals, including humans, often employ different learning mechanisms depending on the context or domain in which they confront a task (for reviews, see Hauser 2000; Hirschfeld and Gelman 1994; Rozin and Kalat 1971). These mechanisms differ, in part, because they cause the animal to attend to different features of a problem in different domains. For example, in studies of cotton-top tamarins (*Saguinus oedipus*), results indicate that individuals attend to shape over color in tasks involving tools (Hauser 1997; Hauser et al. 1999). In contrast, in studies of rhesus monkeys (*Macaca mulatta*), subjects attend to color over shape in a task involving food (Santos et al., in press). Specialized learning mechanisms may guide the acquisition of spatial knowledge by constraining the kinds of experience or input to which animals attend (Cheng 1986; Gallistel 1990; Hermer-Vazquez et al. 1999; Spelke and Newport 1998; Spelke and Tsivkin, in press).

For the domain of spatial cognition, we can ask: what properties or features of spatial objects make them reliable landmarks? Research on rodents and pigeons in particular shows that while spatial constancy (e.g., Biegler and Morris 1993) may emerge as a dominant feature, other object properties may also be incorporated into the representation of a landmark (Cheng and Spetch 1998; Collett et al. 1986; Etienne et al. 1998). With respect to primates, much less is known. For example, long-tailed macaques (*Macaca fascicularis*) search near structures of the same category for which they initially discovered food, and when they find food on the ground that is typically found in the trees' canopy, they look up (Menzel 1996, 1997). Similarly, when wild moustached tamarins (*Saguinus mystax*) find a tree laden with fruit, they will search for other trees of the same species (Garber 1993). These observations suggest that some monkeys attend to features of the landmarks and targets that are relevant and reliable in the context of foraging.

Primate studies have also revealed that the spatial location of an object may be more important than other object features (Gouteux et al. 1999). For instance, Menzel and Menzel (1979) found that after being habituated to an object in one location, marmosets (*Saguinus fuscicollis*) responded more strongly (i.e., increase their exploratory or investigative behavior) to a change in a landmark's location than to its orientation. The marmosets also responded more strongly to a change in object identity, especially when the object was located in its original position, than to changes in the object's orientation and position. This finding supports the idea that marmosets attend to a variety of object properties, though to some features (i.e., identity) more than others (i.e., orientation). Garber and Dolins (1996) obtained similar results while studying foraging in wild moustached tamarins. They presented the monkeys with 16 platforms, half empty and half containing bananas on a given day; the same platforms were baited for four consecutive days. Although the tamarins' ability to find the baited platforms was above chance, their performance increased to 100% once the baited platforms were marked with red flags. However, when the experimenters baited different platforms, the tamarins returned to the originally baited locations; this foraging pattern emerged even though the experimenters marked the newly baited locations with the flags. These results suggest that the positional information superseded the visual information offered by the objects. It is also possible that the monkeys lacked sufficient experience with the red flags, and consequently, failed to encode them as reliable predictors of food location; this alternative explanation is consistent with the idea that positional constancy is fundamental to a landmark's reliability.

The present experiment addresses the problem of whether and how animals integrate geometric and non-geometric features in a foraging task, and the relative importance of different features in the identification of a reliable landmark. We trained cotton-top tamarins to search in a three-dimensional laboratory "jungle" for food located several centimeters above or below a colored pole landmark. In this experiment, we considered the food-landmark relation as a geometric feature and the landmark itself as a non-geometric feature. Once monkeys learned to use the colored pole to find food located at a specific distance, we asked whether their search strategies would change when we altered (1) the spatial relationship between landmark and target, and (2) the landmark's properties (color, shape, identity and location). In parallel with studies by Menzel and Menzel (1979) on marmosets, and by Gouteux et al. (1999) on baboons, we used the tamarins' exploratory behavior to understand which features of a landmark are most salient. We expected to find greater exploratory behavior at or near the landmark as a function of increasingly salient alterations to the original landmark, and hypothesized, based on the findings of such experiments as Menzel and Menzel (1979), that identity and shape would be more crucial landmark features than color or orientation, therefore eliciting a greater response.

In addition to studying the relative importance of different landmark features, we also investigated the flexibility of the tamarin's spatial representation by exploring (1) whether the geometric information (i.e., above or below) acquired in the first set of conditions could be used to find food in a novel location, both with respect to distance from the landmark and with respect to the overall geometry of the space; (2) the capacity to generalize from one exemplar to many by presenting tamarins with two familiar objects or potential landmarks; and (3) the ability to discriminate familiar from novel objects, approaching the familiar landmark first. If the tamarin's initial representation of this spatial task is strictly associated with specific perceptual features (e.g., food is located a specific distance *x* above or below the landmark; the landmark is an upright red pole), then they will have difficulty finding the food in the probe trials. In contrast, if the tamarins' spatial system is more flexible, then they should have little difficulty generalizing to new distances from the landmark, to changes in the overall geometry of the search space, and to featural manipulations of the landmarks.

Method

Subjects

Subjects were ten cotton-top tamarins, a New World monkey species endemic to the neo-tropical rainforests of northern Colombia. In their natural habitat, they feed primarily on insects, fruits and nectar, and prefer tree species with specific characteristics including small to moderately sized crowns, intra-specific fruiting synchrony, and a small amount of fruit available each day (Garber 1993). Because of these qualities, the monkeys must exploit a set of temporally predictable fruiting trees, such that during a day, they will typically exploit one individual tree species, eating fruit from that kind of tree over the entire range (Garber 1993).

All of our experimental subjects were acquired from the New England Regional Primate Research Center in Southborough, Massachusetts. They have lived in captivity all of their lives, housed in social groups at the Primate Cognitive Neuroscience Laboratory at Harvard University. The colony room is divided into six families, each family occupying a stainless steel cage measuring 1.8 m high×1.4 m wide×0.7 m deep; each cage is filled with a lattice of branches from local trees, ropes, and wooden nest boxes. While spatially separated, the families can see each other and communicate with olfactory, visual, and auditory cues. Monkeys have ad libitum access to water, and are fed Zupreem monkey chow, insects, fruit, and nuts at the end of the day, after the experiments have been run.

The tamarins participate in noninvasive behavioral experiments during the day, from 0800–1800 hours. All subjects have participated in experiments, mostly on object perception as well as communication. For example, using a means-end reaching task, experiments show that tamarins can use simple tools to gain access to food (Hauser 1997; Hauser et al. 1999). Other experiments in the laboratory have used the expectancy violation procedure, habituation-dishabituation, and traditional operant techniques to explore human speech perception, face processing, and the attribution of goal directed attention (Ramus et al. 2000; Santos and Hauser 1999; Weiss et al. 2001). Although our subjects are clearly not experimentally naïve, the present experiments represent the first experimental tests of spatial knowledge in a foraging task.

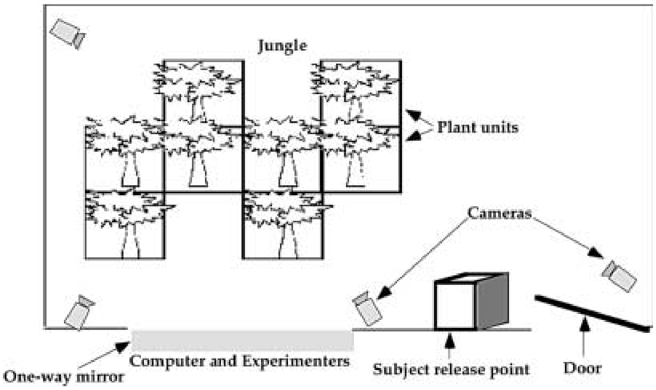

Fig. 1 A schematic illustration of the three-dimensional "jungle" apparatus used with cotton-top tamarins

We divided our subjects into two groups. Six received the "Above landmark" condition (Above group), and four received the "Below landmark" condition (Below group). The Above group consisted of four females and two males, and the Below group consisted of two females and two males.

Apparatus

The experimental room (Fig. 1) was 2.1×4.0 m^2 and consisted of three solid walls and one curtained wall. The release point was located in between the door and the mirror. A "jungle" was constructed out of eight identical rectangular structures (each unit measuring 0.6×0.6 m^2 at the base and 1.5 m high) made of PVC piping, wooden poles and planks. Wooden poles were placed at a horizontal angle into the piping, a foot apart from each other, beginning a foot above the ground; this created four ladder-like surfaces on each face of the rectangular prism. Wooden boards, 10.2 cm wide by 1.3 m thick, were screwed into the poles to create planks on which landmarks could be placed. Plastic green leafy plants, approximately 1.5 m high, were placed inside the structure and stabilized by bungee cords. Each structure comprised one "plant unit," and was tied to another unit to create a pair. These pairs were organized into a zigzag pattern as shown in Fig. 1.

The landmarks were objects made from PVC piping, foamcore, and brightly colored masking tape. The colors included yellow, red, blue, and pink, and the shapes included poles (0.3 m high, 5.1 cm diameter), boxes (10.2-cm cubes), and triangular prisms (10.2 cm high), each glued to hard plastic disks that could be clipped to the wooden planks. Although it is known that cotton-top tamarins, like other Callitrichids, exhibit dimorphism in color perception (Mollon 1991), with dichromatic males and both dichromatic and trichromatic females, our sample size is too small to explore the effects of this difference on performance. However, in all previous work from our laboratory, we have failed to detect sex differences; this may reflect the lack of a sufficiently sensitive assay rather than the lack of an effect.

Procedures

For the monkeys in the Above group, we placed half of a mini-marshmallow on a leaf directly above a vertically positioned, upward-oriented landmark[1]. For the Below group, we placed half of

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[1] We note here that because the food reward was placed close to the target object, this particular kind of landmark is perhaps best referred to as a beacon; for consistency with the rest of the paper, however, we continue to use the term landmark

Fig. 2 **A** Subjects were initially trained to find food either above or below a *pole* (i.e., landmark) attached to a surface of the jungle. The food was affixed to a leaf either above or below the pole. Records of the tamarin's foraging movements were obtained, delineating three locations: *Correct Area* (i.e., either above or below the pole), *Landmark Area* (i.e., at or next to the pole), and *Incorrect Area* (i.e., either below the pole for the "Above group" or above the pole for the "Below group"). **B** A *tamarin* searching for food *above the pole*, and a *tamarin* searching *below the pole*

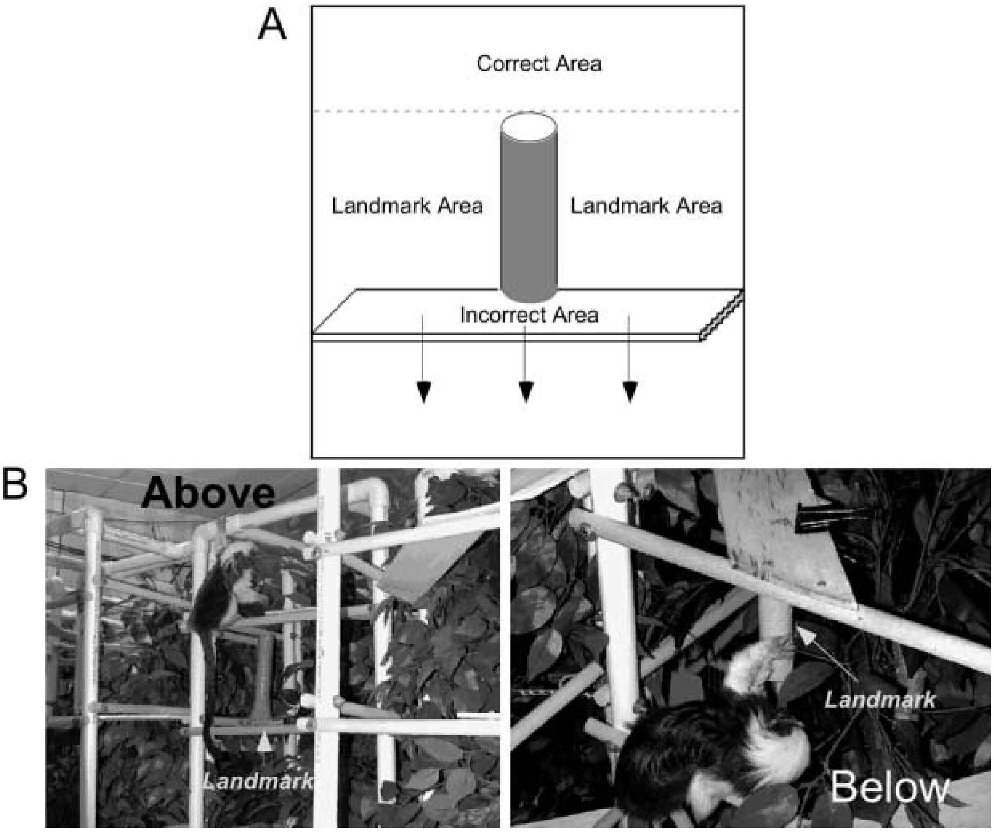
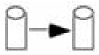
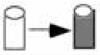
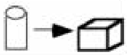


Table 1 Probe conditions used to test for salience of different landmark features

Probe condition	Original	Orientation	Color	Shape	Novel Identity
Example *Original -> Feature change*					

a mini-marshmallow on a leaf directly below a vertically positioned, downward-oriented landmark (Fig. 2A, B).

The experiment consisted of three phases, two training phases and a test phase. All sessions included five trials, and monkeys received no more than one session each day. All trials ended either when the subject found food, or when a set time limit had expired. In all reinforced trials, we hid the marshmallow either on the top or the bottom of a leaf. During the training phases, we placed the food and landmark in one of two possible locations in the jungle based on the output of a random number generator. During the test phase, we used eight possible locations for the food and landmark, including the two original locations. We always set up the landmark and food out of view of the subject.

For the first training phase, we hid the marshmallow 2.5 cm from the tip of the landmark on a leaf, and allowed subjects 5 min to find the food. Subjects moved on to the second training phase once they had successfully retrieved the food during ten consecutive trials or two complete sessions. During the second training phase, we increased the distance between the landmark and the food to 10.2 cm, decreased the time limit to 3 min, and inserted one unreinforced trial randomly into each five-trial session to eliminate the novelty of future unreinforced probe trials. Subjects moved to the test phase once they had retrieved the food on 15 consecutive trials (i.e., 3 sessions), excluding the unreinforced trials.

The test phase consisted of 3-min trials with food placed 10.2 cm from the landmark (except in some probes, discussed later); in contrast to the training trials, we increased the number of possible locations of the landmark from two to eight during the test trials. For the first trial in each session, we always placed the landmark and food in one of the two original (i.e., training) locations. For the next four trials, the position of the landmark varied randomly among the eight possible locations. Of these four trials, we randomly selected one to be a "probe trial" in which we altered some feature of the landmark or distance to food. Every monkey received two trials of every probe, with order of probes counterbalanced across subjects. When an individual failed to retrieve the food, we ran them again under the same condition until they succeeded; this only occurred on one trial each for eight of the ten subjects, and not at all for the other two subjects.

Probe trials were either reinforced or unreinforced. Unreinforced probe trials lasted for 3 min, with an object placed in one of the eight possible locations. The unreinforced probes included a familiar condition involving the originally trained landmark object, and trials in which we varied one or more features of the original landmark object; specifically, we changed the orientation, color, shape and overall identity (color and shape) of the landmark (Table 1).

Reinforced probe trials generally involved the original landmark, but altered the relationship between the food and the object (Table 2). These probes included manipulations of landmark number, jungle configuration, original versus novel object, distance (occluded and visible), and a no-landmark condition. Table 2 presents a summary of our probe conditions and explains the theoretical motivation underlying our choice of conditions.

All trials were videotaped, and one experimenter followed the path of the monkey through the jungle with a computer program that recorded timed coordinates of the subject on a map; all observations were made from a one-way mirror, such that tamarins foraged without any humans in the room. The other experimenter

Table 2 Examples and description of reinforced probes using the original landmark, and changes in the number of landmarks, distance to food, jungle configuration, and distracter objects

Probe condition	Description	Scored "correct" if:
Number	Two original landmarks baited; test to see if subject can generalize to multiple landmarks of the same kind.	Subject finds both pieces of food within 3 min.
Rearranged jungle	Scrambled configuration of plant units; original landmark baited and placed in novel location; test to see if subject can generalize to novel environment with different external geometry.	Subject finds food within 3 min.
Familiar vs. Novel object	Baited original landmark and placed novel object in equally visible areas; test to see if subject distinguishes the original landmark from other objects and prefers to search original object first, and longer.	Subject approaches the original object first, within 3 min.
Distance (visible)	Expanded landmark-food distance to 30.5 cm; food on same side of leaf as landmark, i.e., visible from the landmark; test to see if subject can generalize after changes in scale.	Subject finds food within 3 min.
Distance (occluded)	Expanded landmark-food distance to 30.5 cm; food on opposite side of leaf as landmark, i.e., not visible from the landmark; test to see if subject can generalize after changes in scale.	Subject finds food within 3 min.
No landmark	No landmark, but food is hidden in one of the eight familiar locations; control test to see if subject is actually using landmarks or finding food by chance in the vicinity of the landmarks.	Subject finds food within 3 min.

recorded the direction of the subject's gaze once it had come within 0.3 m of the landmark; we made these marks every 1.5 s, timed by the ticks of a metronome. We recorded the data on a sheet of paper with a representation of the landmark on the wooden plank, and with the space around the landmark divided into three areas (Fig. 2): (1) below the plank, (2) the landmark itself, and (3) above the plank and landmark. For the Above group, area 3 was considered the "correct" region, whereas area 1 was "incorrect". For the Below group, in contrast, area 3 was incorrect and area 1 was correct.

Data analysis for the unreinforced probes included counting the number of marks in each of the three foraging areas. The total number of marks for all areas made within 3 min, multiplied by 1.5, gives the Total Time the monkey spent searching within 0.3 m of the landmark. The number of marks in the correct region divided by the total number of marks in all regions yields the Correct Ratio which indicates the proportion of time the monkey spent searching in the appropriate region when within 0.3 m of the landmark. Similarly, the Landmark Ratio is the number of marks in area 2 or the landmark region divided by the total number of marks in all regions; this measure indicates the proportion of time the subject looked directly at the landmark while within 0.3 m of it. Finally, the Incorrect Ratio is the number of marks in the incorrect region divided by the total number of marks in all regions; this measure signifies the fraction of time a subject spends searching in the inappropriate location.

For the unreinforced trials, we compared subjects' search patterns on the original landmark with each of the probes involving a featural change; we expected search patterns to differ under those conditions where the featural change was salient to the tamarins (i.e., where the new feature changes the reliability of the object as a landmark). For the reinforced probe trials, we compared the search patterns on each probe against the "no landmark" condition to assess whether the tamarins were using the information provided by the novel probe conditions.

As a final control, we tested three naïve monkeys (i.e., no experimental experience in any of the foraging tasks in the jungle set up) with two trials involving the original landmarks, but in the absence of food. Each monkey received one 3-min trial with a colored pole oriented as for the Above group and one 3-min trial with a colored pole positioned as for the Below group. We counterbalanced the order in which the monkeys received these trials. The purpose of these controls was to assess whether tamarins have an inherent bias to search at, above, or below a novel object placed in a foraging environment, and whether olfactory cues alone might be sufficient to find the food reward in the absence of any landmark information.

Results

Subjects reached criterion on the training phase (i.e., food placed within 2.5 and 10.2 cm or on the landmark, with the landmark placed in one of two locations) of this task after a mean of 41.0 trials (SE=14.5, range 20–60). The difference in the number of training trials required by the Above group (mean=35, SE=12.24, range 20–50) and the Below group (mean=50, SE=14.14; range 30–60) was not significant (t_8=1.79, *P*=0.11). Subjects required, on average, 115.4 trials (SE=7.1, range 109–132) to complete all the test sessions involving the 11 probe trials (including the 5 unreinforced and 6 reinforced probe trials) run twice each. Again, the difference in the mean total number of test trials for the Above group (mean=113.3, SE=4.63, range 109–121) and the Below group (mean=118.5, SE=9.68, range 111–132) was not statistically significant (t_8=1.15, *P*=0.28).

To determine how well the trained monkeys learned to search, we compared the results from their unreinforced familiar trials to the performance of the naïve monkeys, and contrasted the trained monkeys' performance during reinforced non-probe trials to their behavior in the no landmark condition. The three untrained monkeys spent on average 9.3 s (SE=5.8, range 6–16 s) within a 0.3-m radius of the landmark in the Above condition, and 1.7 s (SE=2.1, range 0–4 s) during the Below condition. Overall, the monkeys spent 93% of the time (SE=17, range 62–100%) attending directly to the landmark, a value calculated by dividing the amount of time spent looking at the landmark by the total amount of time spent near it (the Landmark Ratio). In contrast, once the ten experimental monkeys reached criterion during training and learned to use the landmarks to locate food, they spent 28.0 s (SE=2.23, range 11.0–43.5 s) within a foot of the landmark during the 3-min unreinforced trials with their familiar landmark and 80% of the time (SE=3%, range

61–95%) searching in the correct region (the Correct Ratio). There was a significant difference between the trained monkeys' and naïve monkeys' mean total times (t_{11}=3.65, P=0.004) and correct ratios (t_{11}=–9.40, P=0.0001), indicating that after training, search patterns changed significantly.

A second indication of the degree to which the monkeys had learned the task is the difference between reinforced trials with the familiar landmark and the no landmark trials in which food was hidden in one of the eight possible locations, though without an object to mark its location. During the two no-landmark trials each subject received, seven monkeys never found food, two monkeys found food in one of two trials, and 1 subject found food in both trials, yielding an average failure rate of 80%; these results show that olfactory cues are not sufficient for locating the food. For the no-landmark trials in which the monkeys did find food, it took an average of 137.5 s (SE=43.4, range 83–173 s). In contrast, for non-probe reinforced test trials, monkeys spent on average only 33.0 s (SE=7.3, range 17.5–39.1 s) before finding the food; overall, subjects failed to find food in only 0.1% of all trials run (range 0–1.8%). For these two conditions, there were significant differences between the failure rates (paired: t_9=7.16, P=0.0001) and the time required to locate food (unpaired: t_{12}=7.81, P=0.0001).

To explore whether subjects first searched in the originally trained locations (a pattern that would fit with their perseverative biases or a win-stay/lose-shift strategy) or attended to the position of the landmark, we ran a repeated measures ANOVA across the first ten sessions of the test phase with session (1–10) and position searched (correct or incorrect) as within subject factors. We found a main effect of position ($F_{1,81}$=126.00, P=0.0001). Subjects searched more in the correct location (mean=2.16) than the incorrect location (mean=0.2). There was also a significant interaction between session and position ($F_{9,81}$= 2.63, P=0.01). Although searching in the correct location does not differ across session, subjects searched less in the incorrect location as the sessions went on. Consequently, subjects did not pursue a win-stay/lose-shift strategy, but rather, used the landmark to find food.

To examine how well monkeys generalized to novel conditions, we used Wilcoxon Signed Rank tests for the baited probe trials. To interpret how featural changes in the object affected subjects' searching during the unreinforced probes, we performed ANOVAs comparing the unreinforced probe trials to the unreinforced familiar trials. We analyzed the total time subjects spent near the landmark, and the proportion of that time they spent looking in the appropriate region (Correct Ratio), at the landmark itself (Landmark Ratio), and in the inappropriate region (Incorrect Ratio).

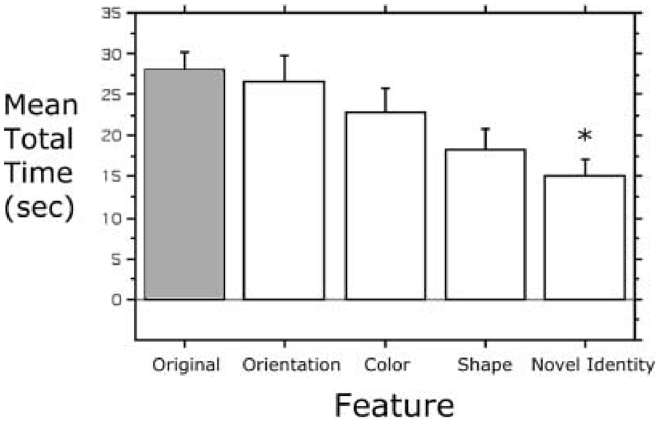


Fig. 3 Mean amount of time (s) tamarins spent within 0.3 m of the landmark for each of the featural changes. *SE bars* presented, *statistically significant difference in comparison with original (*filled column*)

We performed an ANOVA to examine the total times in each of the unreinforced 3-min probe conditions with Feature (familiar, orientation, color, shape, and novel identity) and Order as within-subjects variables, and Above/Below (i.e., group) as a between-subjects variable. There was no main effect of Above/Below ($F_{1,8}$=0.006, P=0.94) or of Order ($F_{1,8}$=0.41, P=0.54), indicating that Above and Below monkeys performed similarly and that each subject performed similarly on the first and second exposures to each probe. There was also no interaction between Above/Below and Feature ($F_{4,32}$=0.42, P=0.80) or between Order and Feature ($F_{4,32}$=1.83, P=0.15), suggesting that there was no difference between the pattern observed in both groups or the pattern observed in the first and second round of probes for all monkeys. Similarly, there was no interaction between Feature, Above/Below, and Order ($F_{4,32}$=0.59, P=0.67).

There was, however, a significant effect of Feature ($F_{4,32}$=4.81, P=0.004), indicating that there was some difference across the probe conditions. Figure 3 shows the average amount of time monkeys spent within 0.3 m of the landmark for each condition. We performed ten contrasts to examine the differences between the probe conditions, and thus, using a Bonferroni procedure, adjusted our alpha level to α=0.05/10=0.005. The monkeys' foraging behavior was most similar to the unreinforced original condition when either orientation or color was altered, and most different when either shape or identity (both shape and color) was changed. The contrasts comparing the mean total time spent during each unreinforced probe condition against the mean total time spent during the original trials revealed no significant differences between the familiar trials and either the orientation, color, or shape probe trials (orientation: $F_{1,32}$=0.12, P=0.74; color: $F_{1,32}$=1.75, P=0.20; shape: $F_{1,32}$=7.22, P=0.01), but a significant difference with the novel identity probe trial (novel identity: $F_{1,32}$=13.34, P=0.0009). Further contrasts between all the unreinforced probe conditions revealed that the only significant difference was between the orientation and novel identity probes ($F_{1,32}$=10.97, P=0.002). A few contrasts approached significance (orientation-shape: $F_{1,32}$=5.51, P=0.03; color-novel identity: $F_{1,32}$= 5.42, P=0.03), but all others were not significant (orientation-color: $F_{1,32}$=0.97, P=0.33; color-shape: $F_{1,32}$=1.86, P=0.18; shape-novel identity: $F_{1,32}$=0.93, P=0.34). In gen-

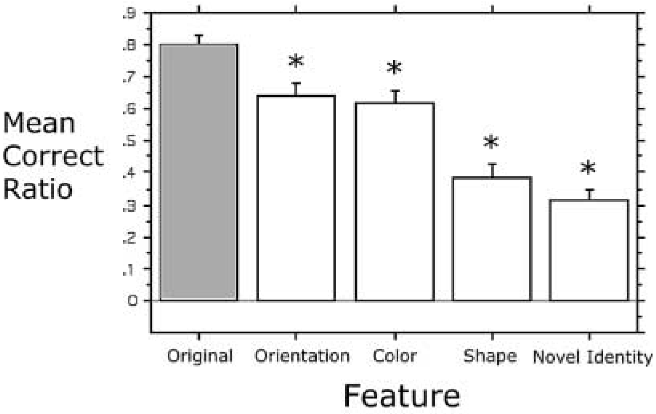


Fig. 4 Mean Correct Ratio scores for tamarins as a function of each of the featural changes. *SE bars* presented, *statistically significant difference in comparison with original (*filled column*)

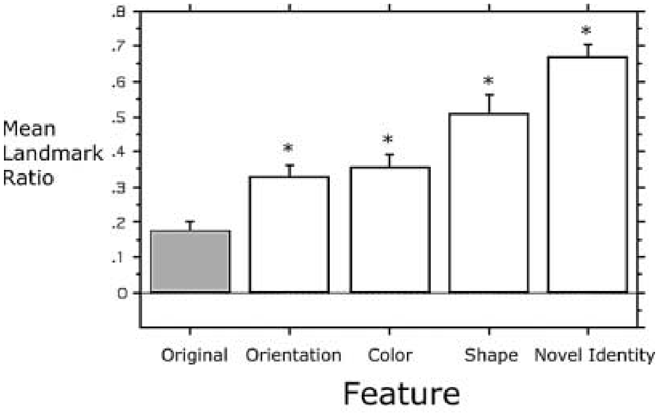


Fig. 5 Mean Landmark Ratios for tamarins as a function of each of the featural changes. *SE bars* presented, *statistically significant difference in comparison with original (*filled column*)

eral, the tamarins appeared to perceive these features differently, such that some manipulations (orientation, color, shape) had little effect on their foraging patterns, while others (identity) had a significant effect.

To determine the accuracy of the tamarins' search behavior, we analyzed the proportion of time spent looking in the correct region of space by dividing the time spent looking in the appropriate area by the total amount of time within 0.3 m of the landmark (i.e., the Correct Ratio). The Correct Ratio in the familiar unreinforced condition was 0.80 (SE=0.03). We performed an ANOVA comparing the mean Correct Ratios for each of the probe conditions with Feature and Order as within subjects variables and Above/Below as a between subjects variable. There was no main effect for Above/Below ($F_{1,8}$=1.55, P=0.24) and no interaction between Above/Below and Feature ($F_{4,32}$=1.09, P=0.38), indicating no difference between the groups. There was a significant main effect of Order ($F_{1,8}$=8.63, P=0.02), such that subjects spent a greater proportion of time searching in the correct location in the second exposure to probes than the first, an effect possibly related to the monkeys' higher expectation of finding food due to added experience. However, there was no interaction between Feature and Order, ($F_{4,32}$=2.24, P=0.09), such that the effect observed was similar for the first and second round of probes. Also, there was no interaction between Feature, Order, and Above/Below ($F_{4,32}$=1.03, P=0.41).

There was a significant difference across the probe conditions for the mean Correct Ratios ($F_{4,32}$=26.10, P=0.0001). A similar trend appears as for the mean total times, such that tamarins responded in the same way to the orientation and color probes as they did to the familiar unreinforced trials, and responded differently to the shape and identity probes (Fig. 4). We conducted ten contrasts with the α level set at 0.005, and found that all probe condition means differed significantly from the familiar condition (orientation: $F_{1,32}$=9.40, P=0.004; color: $F_{1,32}$=11.33, P=0.002; shape: $F_{1,32}$=55.14, P=0.0001; novel identity: $F_{1,32}$=80.63, P=0.0001). Furthermore, all other contrasts revealed significant differences (orientation-shape: $F_{1,32}$=19.00, P=0.0001; orientation-novel identity: $F_{1,32}$=34.97, P=0.0001; color-shape: $F_{1,32}$=16.48, P=0.0001; color-novel identity: F(1, 32)=31.51, P=0.0001), except the tests comparing orientation and color ($F_{1,32}$=0.09, P=0.77) and shape and novel identity ($F_{1,32}$=2.41, P=0.13). The tamarins appeared to notice all featural changes, but to different degrees. Results from the orientation and color probes were not significantly different from each other, but both differed from shape and novel identity, confirming the patterns from the mean total times. Overall, there appeared to be a significant trend: when orientation or color has been altered, tamarins spend more total time near the landmark and more time searching in the appropriate area, either above or below the object; when shape or identity have been altered, tamarins spend less time searching.

Complementing the pattern obtained with the Correct Ratios, we found the opposite effect for the Landmark Ratios (i.e., time spent looking directly at the landmark divided by the total time spent within 0.3 m of the object). Monkeys scored the lowest Landmark Ratios during the familiar trials (mean=0.17; SE=0.02); the mean proportions increased over the probe trials in the following order: orientation, color, shape, and novel identity (Fig. 5). We performed an ANOVA for the Landmark Ratios with Above/Below as a between subjects variable and Order and Feature as within subjects variables. There was no main effect of Above/Below ($F_{1,8}$=4.34, P=0.07) and there was no significant interaction between Above/Below and Feature ($F_{4,32}$=1.17, P=0.34), indicating that both groups responded in a similar way. There was no interaction between Above/Below, Order, and Feature ($F_{4,32}$=0.950, P=0.45).

Results further revealed a significant difference in the mean Landmark Ratios between probe conditions ($F_{4,32}$=20.33, P=0.0001). Ten contrasts at the α=0.005 level revealed that all probe conditions except orientation differed significantly from the familiar condition (orientation: $F_{1,32}$=7.12, P=0.01; color: $F_{1,32}$=9.70, P=0.004;

shape: $F_{1,32}$=29.06, P=0.0001; novel identity: $F_{1,32}$=72.15, P=0.0001). Also, all probe conditions differed significantly from each other (orientation-novel identity: $F_{1,32}$=33.93, P=0.0001; color-novel identity: $F_{1,32}$=28.94, P=0.0001; shape-novel identity: $F_{1,32}$=9.63, P=0.004), except for the orientation-color comparison ($F_{1,32}$=0.198, P=0.66), the orientation-shape comparison ($F_{1,32}$=7.41, P=0.01), and the color-shape comparison ($F_{1,32}$=5.18, P=0.03). Again we observed a ranking of features, such that tamarins perceived changes in shape and identity as the most salient alterations, whereas changes in orientation and color represented the least salient changes.

An ANOVA for the Incorrect Ratio means, calculated by dividing the time spent searching in the incorrect region (below for the Above group, and above for the Below group) by the total time spent within 0.3 m of the object, revealed a non-significant difference between the means for the various conditions ($F_{4,32}$=0.191, P=0.94). Typically, monkeys spent almost no time searching in the incorrect area around the object once they had been trained, independent of condition.

To test whether tamarins could generalize from what they had learned, we compared performance on probe trials in which the landmark was baited with probe trials in which there were no landmarks. Out of the ten subjects tested, seven monkeys never found food, two monkeys found food in one of the two trials, and one subject found food in both no landmark trials. Results from a Wilcoxon Signed Rank test, set up to compare each monkey's performance in this condition to their scores during the reinforced number probes, revealed a significant difference (Z=2.67, P=0.008) with nine monkeys performing better in the landmark than the no landmark condition and one monkey performing equally well. The monkeys also performed significantly better in the rearranged jungle probe (see Table 2 for probes) than in the no landmark condition (Z=2.66, P=0.008), with nine subjects showing the effect and one showing no difference. Comparing the no landmark condition to the Familiar versus Novel identity test revealed a significant difference (Z=2.52, P=0.01), with eight monkeys performing better in the latter condition and two showing no difference. The monkeys performed significantly better in the distance (visible) than in the no landmark probe (Z=2.67, P=0.008), with nine monkeys showing the effect and 1 monkey showing no difference. A signed rank test comparing performance in the distance (occluded) and no landmark trials indicated no significant difference (Z=0.93, P=0.35), with five monkeys performing better in the distance trials, two monkeys performing worse, and three monkeys showing no difference. For the distance (occluded) condition, two monkeys found food in both trials, four monkeys found food in one of two trials, and four monkeys failed to find food at all.

Discussion

Adult cotton-top tamarins learned to search for food above and below a specific landmark, generalized their search patterns to a novel environmental shape (e.g., the rearranged jungle probe) and to multiple landmarks, and showed discrimination of objects based on the functional significance of particular features. Tamarins appeared to begin each trial looking for an object that matched their representation of the familiar landmark, independent of the immediate situation. Once they located such an object, they searched in the appropriate space, either above or below depending upon their training experience. Analyses of time spent near the landmark revealed that some featural changes to the object (e.g., color, orientation) had no perceptible effect on the tamarins' foraging patterns, whereas other changes (i.e., shape, identity) were significant.

As reviewed in the Introduction, there are many studies showing that animals use landmarks during navigation, and more importantly, use particular features to determine what constitutes a reliable landmark. Other studies have shown that animals attend to the geometry of a space to locate target objects or areas, reflecting their capacity to compute the metric relations between spatial elements. Relatively fewer studies have explored the capacity to integrate information from both geometric and non-geometric features in order to solve a spatial task (Cheng 1986; Collett et al. 1986; Gallistel 1990; Gouteux et al., in press; Hermer-Vazquez et al. 1999; Kelly et al. 1998; Spetch et al. 1996, 1997; Vallortigara et al. 1990). In the present experiments, we asked whether tamarins are capable of integrating information about the relative position of food above or below a landmark, with information about the landmark's identity. We picked this particular geometric relationship, rather than the external geometry of the foraging space, because we considered it to be more ecologically meaningful. Specifically, given that tamarins are arboreal animals that live naturally in a dynamically changing rainforest environment, we expected the surrounding shape of the foraging environment to be less important than the relative position of food above or below a landmark. Results revealed that the tamarins integrated information relating the landmark to food (above/below) with the information distinguishing the landmark (blue pole) from other objects. Being able to recognize a type of tree by some kind of feature or "landmark" is crucial when different types of trees bear fruit at different times, as they do in tamarins and other species (Garber 1993; Garber and Dolins 1996; Menzel 1996, 1997). Similarly, tying together an object's featural properties with its geometric relation to a goal is fundamental for species like tamarins where the search space consists of a three-dimensional volume; similar foraging demands are likely to occur in other species as well (e.g., Kamil and Jones 1997).

An important goal of our experiments was to determine how cotton-top tamarins recognize and identify a landmark. Results showed that changes in orientation and color do not alter the perceived reliability of an object as a landmark, while changes in the shape or identity of an object apparently render the object unreliable as a landmark. Tamarins spent less overall time and less proportional time searching in the location indicated by the original landmark when the object changed shape or identity than when it changed color or orientation. When confronted with both a novel identity and the familiar landmark, tamarins almost always approached the correct landmark first and then found the hidden food. It is clear that the tamarin's representation of the landmark is fairly specific, and that monkeys encode the essential features that make an object a reliable indicator of a target's location.

By documenting which featural properties are most important for recognizing a landmark, we add to our growing understanding of object knowledge in cotton-top tamarins and other primates as well. Thus, our own studies of tamarins, together with studies of baboons and rhesus (Gouteux et al. 1999, in press), show that at least some primates can integrate featural information about a landmark with information about the geometry of a search space, or the geometrical relationship between a landmark and a target reward. Moreover, these studies also show that the shape of a landmark is critical to its identity, whereas color is either irrelevant or significantly less important. As such, the tamarin's representation of a landmark and of a tool are similar in that each consider shape as a functionally relevant feature and color as a functionally irrelevant/insignificant feature (Hauser 1997; Hauser et al. 1999); what distinguishes these two domains is that orientation is important for tools, but not for landmarks. In contrast with these two domains, studies of rhesus monkeys indicate that for food, color is a functionally relevant feature whereas shape is not (Santos et al., in press); studies like these are underway with tamarins. Ultimately, these studies will help inform our understanding of the mechanisms underlying different domains of knowledge, and how they are acquired over time, both evolutionarily and developmentally (Hauser 2000).

A second goal of the present experiments was to explore the possibility of relatively abstract spatial representations. What we mean by abstract is that the representation is more conceptual than perceptual. Thus, a perceptual representation of "above" would be revealed by a subject searching a fixed distance above a specific landmark, and showing little to no evidence of generalizing from the distance and object used in training. In contrast, a conceptual representation of above would be revealed if a subject searched for food over a variable set of distances from a variable set of objects that constitute similar landmarks; for example, subjects search at distances both less than and greater than those used during training, and can use objects that are functionally similar to those used in training. We take the recent experiments by Kamil and Jones (1997) on Clark's nutcrackers to constitute evidence for an abstract conceptual representation of "middle". In our experiments, subjects successfully foraged for food 2.54 and 10.2 cm away from a red pole hidden in two locations over training. Despite the lack of variability in these training conditions, however, the tamarins generalized to some novel situations. Specifically, the tamarins' ability to search above or below a landmark appeared independent of the specific learning context, as demonstrated by the probe trials in which the jungle apparatus itself was dissembled to create a new, unfamiliar form of the jungle, and by the test trials in which the landmark and food were together placed in novel locations and distances within the familiar jungle environment. The fact that there was a decrement in performance on some of the distance probes shows that the tamarins were using distance and metric information, but were in part limited by the initial training regime. Moreover, the tamarin's representation of the landmark was not restricted to a specific object (i.e., specific features) as evidenced by the fact that they were equally efficient in finding food when the object's orientation and color changed from the original.

We conclude with three points. First, tamarins can integrate geometric and non-geometric information in at least one spatial foraging task. Second, the features used to establish a reliable landmark are different from the features used to identify objects in other domains. Third, future work will explore whether the capacity to integrate geometric and non-geometric information extends to other spatial tasks, such as reorientation following disorientation.

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