

Sensory information and associative cues used in food detection by wild vervet monkeys

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Abstract Understanding animals' spatial perception is a critical step toward discerning their cognitive processes. The spatial sense is multimodal and based on both the external world and mental representations of that world. Navigation in each species depends upon its evolutionary history, physiology, and ecological niche. We carried out foraging experiments on wild vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda, to determine the types of cues used to detect food and whether associative cues could be used to find hidden food. Our first and second set of experiments differentiated between vervets' use of global spatial cues (including the arrangement of feeding platforms within the surrounding vegetation) and/or local layout cues (the position of platforms relative to one another), relative to the use of goal-object cues on each platform. Our third experiment provided an associative cue to the presence of food with global spatial, local layout, and goal-object cues disguised. Vervets located food above chance levels when goal-object cues and associative cues were present, and visual signals were the predominant goal-object cues that they attended to. With similar sample sizes and methods as previous studies on New World monkeys, vervets were not able to locate food using only

global spatial cues and local layout cues, unlike all five species of platyrrhines thus far tested. Relative to these platyrrhines, the spatial location of food may need to stay the same for a longer time period before vervets encode this information, and goal-object cues may be more salient for them in small-scale space.

Keywords Cercopithecine · Spatial cognition · Sensory ecology · Associative cue · Navigation

Introduction

Our understanding of the ways that animals use environmental and sensory information to navigate has increased markedly over the last two decades. Foraging experiments have been instrumental in revealing important aspects of animals' spatial cognition, especially for wild primates (Garber and Dolins 1996; Garber and Lavallee 1999; Garber and Brown 2006; Janson 1996, 2007, 2011; Bicca-Marques and Garber 2004; Bicca-Marques 2005; Janmaat et al. 2006a, b). Though experiments conducted in the wild cannot be as tightly controlled as those in captivity, they have the advantage of testing questions in a similar environment to which the abilities in question evolved (Janson and Byrne 2007). However, foraging experiments addressing questions of spatial cognition have overwhelmingly been investigated in New World monkeys (platyrrhines, e.g., *Saguinus mystax mystax*, Garber and Dolins 1996; *Cebus capucinus*, Garber and Paciulli 1997; Garber and Lavallee 1999; Garber and Brown 2006; *C. apella nigrinus*, Janson 1996, 2007, 2011; *Aotus nigriceps*, *S. imperator imperator*, *S. fuscicollis weddelli*, *Callicebus cupreus*, Bicca-Marques and Garber 2004; Bicca-Marques 2005). For Old World monkeys

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(catarrhines), spatial perception and the cues used while foraging are much less understood (but see: *Lophocebus albigena johnstoni*, Janmaat et al. 2006a, b; *Papio ursinus*, Noser and Byrne 2007, 2010; Byrne et al. 2009), though some work has been done on lemurs, apes, and humans (e.g., *Propithecus edwardsi*, *Eulemur fulvus rufus*, Erhart and Overdorff 2008; *Hylobates lar*, Asensio et al. 2011; *Pongo pygmaeus*, MacKinnon 1974; *Pan troglodytes*, Normand and Boesch 2009; *Homo sapiens*, Foo et al. 2005). It is essential that a wide range of species are examined because important differences in spatial cognition within the primate order may be revealed (MacLean et al. 2012), especially given variation in sensory systems. This paper aids in redressing the taxonomic bias in foraging experiments on wild primates by replicating previous experiments on platyrrhines (Garber and Dolins 1996; Garber and Lavalée 1999; Bicca-Marques and Garber 2004) on an African monkey (vervet monkeys, *Chlorocebus pygerythrus*). Our goal was to examine the hierarchy of sensory information vervets used in food detection and determine whether they could find hidden food with the use of associative cues. Little is known about spatial perception in vervets (or other cercopithecin monkeys, for that matter), but a tantalizing study by Cramer and Gallistel (1997) on captive vervets showed that they were able to find the shortest route among six sites and that they considered at least the next three site visits before choosing an efficient route (three-step look ahead). This contrasts with some other studies on primates, where individuals looked only one to two steps ahead while making foraging decisions (*Cebus apella*, Janson 2007; *Cercopithecus ascanius whitesidei*; yellow-nosed monkeys, MacDonald and Wilkie 1990; *Pan troglodytes*, Menzel 1973). These results make further investigation into vervet spatial cognition intriguing.

When foraging, animals may use many sensory modalities (i.e., vision, olfaction, audition, tactual perception, electrical perception, echolocation, and proprioception) to perceive the presence of food. For primates, food detection is primarily done through sight, smell, memory of spatial position or some combination of these cues. The relative importance of vision and olfaction for a species depends on their perceptive abilities and the properties of their resources. For instance, early in primate evolution, the acuity and color perception of the visual system was enhanced. Among other changes, the tapetum lucidum was lost in haplorhines, and some primate radiations developed an increase in the ratio of cones to rods in the retina and evolved trichromatic color vision from a dichromatic ancestor (Martin 1990; Jacobs 2009; Isbell 2009). Species with such enhanced visual systems may predominantly rely on vision to locate food. In other species, scent may be most salient in locating food resources, depending on olfactory capacity (Smith and Rossie 2006; Barton 2006), the time of the day spent foraging (Charles-Dominique

1977; Pariente 1979), and the strength and reliability of an odor signal (Vickers 2000). Strepsirrhine primates retain the primitive primate rhinarium and the entire vomeronasal complex (reviewed in: Colquhoun 2011), so their detection of odorants may be greatest within the primate order (e.g., Rushmore et al. 2012). Nonetheless, sensory adaptations may be specific to certain social or ecological signals and may not be transferrable to different situations. For example, functional vomeronasal organs are specific to the processing of pheromonal signals produced by the anogenital glands and do not aid in food detection (Døving and Trotter 1998). In addition to these sensory modalities, memory of the spatial location and positioning of previously used food sources have been shown to play an important role for primates when making foraging decisions (e.g., Garber 1989, 2000; Garber and Lavalée 1999; Bicca-Marques and Garber 2004; Janmaat et al. 2006a, b; Asensio et al. 2011).

Animals are not only confronted with the problem of detecting food when they are near it, they must also find their way, to and from, variable food sources and other important areas of their home range such as sleep sites (Shettleworth 2010). Primates generally use a two-system model for navigation where spatial information can be represented in an egocentric (internal, relative to the body position and direction of motion) and/or an allocentric (external, relative to environmental cues) framework (Wehner and Srinivasan 1981; Etienne et al. 1988, 1998; Gallistel 1990; Wehner et al. 1996; Dolins and Mitchell 2010; but see Wang and Spelke 2002). Use of egocentric representations alone may lead to the accumulation of errors in navigation (Séguinot et al. 1993), and egocentric and allocentric localization appear to work in parallel in most situations to keep an animal oriented (Burgess 2006). The predominant use of one representation over the other may depend upon how much the animal is moving, the size and structure of the environment it is moving through, and prior experience within that environment (Burgess 2006). Egocentric localization can be accomplished by orienting relative to the distance, angle, and direction from an object (or beacon) in space. Allocentric localization can be done by making relational associations between objects (or landmarks) in the environment, independent of an individual's spatial perspective (Dolins and Mitchell 2010). Allocentric representations may be more permanent than egocentric ones because the body position changes as an animal moves, and knowledge of directions in the environment is not gained (Burgess 2006; Waller and Lippa 2007). Associative cues such as beacons and landmarks are used in both egocentric and allocentric navigation by a wide variety of animals including insects (Wehner and Raeber 1979; Cartwright and Collett 1983), fish (Warburton 1990; Cain and Malwal 2002), birds (Balda and Turek

1984; Cheng 1989; Vallortigara et al. 1990; Cheng and Sherry 1992), and mammals (Suzuki et al. 1980; Collett et al. 1986; Cheng 1986; Etienne 1987; Hermer and Spelke 1994; Garber and Dolins 1996; Dolins 2009; Hribar and Call 2011).

In this study, we used foraging experiments to examine food detection in wild vervet monkeys (*Chlorocebus pygerythrus*) in small-scale space, or the area that can be seen from a single vantage point (following Byrne's (2000) definition of "large-scale space"). Specifically, we determined whether global spatial cues, local layout cues, or goal-object cues (Brodbeck 1994) were used by vervet monkeys and whether they could use an associative cue to find hidden food. For our experiments, global spatial cues were more distal and included the relational information provided by the arrangement of feeding platforms and all of the objects, such as trees and bushes, which surrounded them. Local layout cues were more proximal and were provided by the position of certain feeding platforms (e.g., those containing food versus those without food) relative to others. Goal-object cues were those that were provided by the food rewards and other objects placed on the platforms themselves, such as color, texture, or odor (Brodbeck 1994).

Widespread in savannah, woodland, and forest edge throughout sub-Saharan Africa, vervets are among the most adaptable of the cercopithecine monkeys (Cheney and Seyfarth 1992). Now, considered to be several separate species based on their morphology and biogeography (Groves 2001), vervets are both terrestrial and arboreal and are known to be flexible in their diets, eating primarily fruit, insects, and gums in some areas, but supplementing with a range of vegetation and opportunistic feeding on animals (Wrangham and Waterman 1981; Skinner and Smithers 1990). Vervets quite easily adapt to human-modified landscapes, and they are considered pests in many areas for their crop-raiding behaviors (Estes 1992; Saj et al. 2001); however, these habits allow wild vervets to quickly adapt to an experimental study regime.

Our first set of experiments (1A and 1B) sought to determine whether vervet monkeys used goal-object cues more than global spatial cues and/or local layout cues (Brodbeck 1994) when detecting food resources (Table 1; following Garber and Lavalée 1999). We hypothesized that when presented with all of these cues, goal-object cues would be most important for vervets because these allow food to be directly seen or smelled and approached, so navigation does not need to be accomplished with spatial cues provided by objects other than the food in the environment. Of the goal-object cues available, we hypothesized that visual cues would be most salient for vervets because they are catarrhines with an enhanced visual system (Jacobs 2009).

Table 1 Summary of experiments performed on vervet food detection

Experiment	Cues provided	Conditions ^a	Goal	Total # trials
1A	Global spatial, local layout and goal-object	Bananas uncovered, layout of real versus sham rewards remains consistent	Determine how vervets locate food	12
1B	Global spatial, local layout and goal-object	Bananas uncovered, new layout of real versus sham rewards from 1A, layout remains consistent	Determine how vervets locate food	12
Initial switch in the layout of real rewards from 1A to 1B shows whether global spatial and local layout or goal-object cues were used predominantly				
2A	Global spatial and local layout	Bananas covered, banana peels with shams, layout of real versus sham rewards remains consistent	Determine how vervets locate food. Is a win-stay foraging rule used?	12
2B	Global spatial and local layout	Bananas covered, banana peels with shams, new layout of real versus sham rewards from 2A, layout remains consistent	Determine how vervets locate food. Is a win-stay foraging rule used?	12
Initial switch in the layout of real rewards from 2A to 2B informative regarding the extent that global and local cues were used				
3	Associative cue	Bananas covered, banana peels with shams, layout of real versus sham rewards random on each trial, reliable beacon provided	Determine whether vervets use associative cues to food presence	30

Experiments follow those done by Garber and Lavalée (1999)

^a All experiments had three platforms with a real banana and four with a sham (Styrofoam) banana

Our second set of experiments (2A and 2B) examined whether vervets could use global spatial cues and/or local layout cues to locate food resources, without the availability of goal-object cues (Table 1). In these experiments,

vervet monkeys could also have successfully found food by applying a win-stay foraging rule, though this required that they used either global spatial cues or local layout cues to remember the location of food resources. Application of a win-stay rule means that animals return to a particular food source if they have successfully foraged there previously (Garber 1989; Bicca-Marques 2005). If the global spatial position or local layout of food remains consistent, animals can apply previously learned spatial information to predict the location of real rewards in the same spot at a later time. This type of rule may be used whenever animals return to a feeding tree after a certain amount of time to monitor the renewal of resources (Garber and Lavallee 1999) and returning to a platform that previously contained real food indicates that a win-stay rule is being used. We predicted that though goal-object cues would be the dominant means to locate food for vervets, in the absence of these cues, global spatial and/or local layout cues would be used. This implied that vervets would be able to apply a win-stay foraging rule, which has been found to be used successfully by other primates (e.g., *Leontopithecus rosalia*, *Callithrix kuhli*, Platt et al. 1996; *Saguinus mystax mystax*, Garber and Dolins 1996; *S. imperator*, *S. fuscicollis weddelli*, *Callicebus cupreus cupreus*, Bicca-Marques 2005; *Saimiri sciureus*, Andrews 1988; *Cebus capucinus*, Garber and Paciulli 1997; *Cercopithecus ascanius whitesidei*, MacDonald and Wilkie 1990; *Pongo pygmaeus abelii*, MacDonald and Agnes 1999; *Gorilla gorilla gorilla*, MacDonald 1994).

Our last experiment (3) assessed whether vervets could use a nearby, reliable associative cue (a single beacon) to find hidden food resources (Table 1). Use of an associative cue would show egocentric localization by the vervets, who would be defining their axis of orientation relative to the beacon (Burgess 2006). Given that use of associative cues is common throughout the animal kingdom (reviewed in: Spetch and Kelly 2006) and by other primate species (e.g., *Saguinus mystax mystax*, Garber and Dolins 1996; *Cebus capucinus*, Garber and Lavallee 1999), we hypothesized vervets would be able to use these cues for spatial orientation.

Methods

Study site and subjects

This study was conducted at Lake Nabugabo, Masaka District, central Uganda (0°22′–12°S and 31°54′E). Lake Nabugabo (8.2 × 5 km) is a satellite lake to Lake Victoria lying at an elevation 1,136 m. The landscape around the lake is modified by humans and is a matrix that includes wetlands, grasslands, patches of forest, areas with natural

regenerating vegetation, farmers' fields, and a few buildings. One habituated group of vervet monkeys (*Chlorocebus pygerythrus*) at Nabugabo called M group was followed for 2 months (June–July 2012) from dawn to dusk, 5 days per week (41 days). Vervets are ideal subjects for foraging experiments because they are partially terrestrial, eat a varied diet, and easily take food from human sources (Isbell et al. 1998; Saj et al. 2001). This allows experiments to be conducted on the ground and the use of locally grown bananas to be offered as food rewards. The group contained 24 individuals (2 adult males, 5 adult females, 3 subadult males, 3 subadult females, 11 juveniles and infants), and dye-marking was employed at the beginning of the study, after which all individuals could be individually recognized by features of the face and body.

Study design and detailed hypotheses

Experiments used methods and a number of trials similar to Garber and Lavallee (1999) (12 trials for Experiments 1A, 1B, 2A, and 2B; 30 trials for Experiment 3). Individuals were not trained prior to experimentation because their naturalistic foraging behavior and the method with which they found food in each context was of interest. However, depending on the question, the data were analyzed after a certain number of predetermined trials (“learning trials”, see below) to examine the effect of experience on the monkeys' abilities to find food. M group had a predictable daily path, which was partially due to them only using two sleep sites, along the edge of the lake at the NE and SW ends of their home range boundary. Seven feeding platforms, arranged in a circle with each platform 3 m apart, were set up between their sleep sites. The placement of feeding platforms was not changed between trials or experiments, so the global spatial cues (platforms themselves, trees, bushes, etc.) surrounding each platform remained consistent. Platforms were wooden tables approximately 0.75 m high, with a square flat top 0.75 × 0.75 m in size (Fig. 1). The group visited the platforms relatively predictably (usually twice per day) on their way to and from their sleep site. JAT completed 78 trials of five different experimental conditions during the 2 months of observation. After an initial six-day period of habituation to the platforms (Garber and Brown 2006), trials were carried out on most days, whenever the monkeys passed by the platform array (mean number of trials per day: 1.77; range 0–3). It was important for the experimental protocol that the monkeys did not observe the platforms being baited, so all items were placed on the platforms prior to the group's arrival. This usually meant that two trials could not be done in close succession, so trials on the same day were separated by a mean of 7 h and 5 min (range 0:08–12:58). Analyses were done on the

Fig. 1 Experimental set up of seven feeding platforms arranged in a circle, 3 m apart. Platforms are set up for Experiment 1A



number and order of visits to each platform during trials. A visit was scored any time an individual jumped onto one of the feeding platforms. All repeat visits were also scored and the order of visitation was noted. Not all platforms were visited during every trial, depending in part on participants' knowledge of where food was located.

Though vervets are often terrestrial, at our study site they appear more at ease when off the ground or when within a meter or two of the safety of the trees (MMJ White, unpubl. data). We noted that the monkeys tended to run up to the platforms and leap onto the first one in their line of travel, regardless of what was contained on that platform. Indeed, if the platform contents were covered with a leaf, the vervets often did not even lift the leaf to see what was underneath. This suggests that the first platform leaped upon was not always selected as a foraging site, but as a “safe” site. We therefore provide data on the first, second, and third platforms chosen by individual(s) that reached the site relative to the probability that this was a platform with a real banana (Table 2). This approach was also deemed appropriate in the experiments conducted by Garber and Lavalée (1999) and Bicca-Marques and Garber (2004).

Experiments 1A and 1B sought to determine what sensory information vervet monkeys use to detect food resources (Table 1). Global spatial cues, local layout cues, and goal-object cues were all available to the animals. One banana was placed on three of the seven feeding platforms (platform selection done at random), while a sham that resembled a real banana but was made of weighted styrofoam was placed on the other four. The spatial layout of real versus sham bananas was left the same (i.e., spatial location predictable) for 6 days (12 trials). Bananas were left uncovered and provided visual, olfactory, and spatial cues to the monkeys. We hypothesized that the vervets would initially be deceived by the sham bananas, but over

time they would be able to distinguish between real and sham bananas, since all sensory information was available, and would go to platforms containing real bananas, avoiding those with sham bananas more often than by chance (Garber and Lavalée 1999).

In Experiment 1B, all sensory cues were again available to the monkeys. Bananas were again left uncovered (Table 1), with three real and four sham bananas. However, on Day 1 the spatial layout of real and sham bananas was rotated from the set up in 1A and remained the same (i.e., spatial location predictable) for the duration of the experiment (6 days, 12 trials). If global spatial cues and/or local layout cues were foremost in the information used to find food, we hypothesized that the monkeys would initially return to the platforms that had previously contained real bananas in Experiment 1A, showing their transfer of knowledge from the previous condition. Then, over additional trials with the new spatial locations, they would improve in their abilities to locate real bananas, avoiding platforms with sham bananas, at levels greater than chance. If goal-object cues were the most salient in navigating to real food sources, the change in spatial layout was predicted to have no significant effect, initially or in the long-term, on the vervets' ability to locate real food rewards.

Experiments 2A and 2B sought to determine if vervets could use global spatial cues and/or local layout cues to locate food resources without any available goal-object cues (Table 1). On Day 1 of Experiment 2A, the spatial position of three real and four sham bananas was rotated from what it was in Experiment 1B and remained the same (i.e., spatial location predictable) until 12 trials were completed (6 days). However, bananas on all platforms were covered with large leaves to remove visual cues and banana skins were placed with sham bananas so that all platforms smelled like bananas (again following Garber and Lavalée 1999). It was hypothesized that if the spatial

layout of food, in either a global or local context, was used to find real rewards, after a single experiential trial with the new spatial position, the vervets would begin to learn the predictable placement of real bananas, and using a win-stay foraging rule, they would locate real rewards at levels greater than chance.

Experiment 2B provided the same set up as 2A, with global spatial and local layout cues provided and goal-object cues disguised. Three real and four sham bananas were placed on platforms, covered with leaves, with banana skins next to sham rewards; but on Day 1, the spatial layout of the real and sham rewards were rotated from the set up used in Experiment 2A, remaining the same (i.e., spatial location predictable) until 12 trials were completed (6 days; Table 1). Again, if global spatial or local layout cues were used to navigate we predicted that, on their first trial with the new reward locations, the monkeys would initially return to platforms that previously contained real food, showing transfer of spatial knowledge from the previous condition. Then, after a few trials and using the win-stay foraging rule, they would get better at locating food and would go to platforms with real rewards at levels significantly greater than chance (Garber and Lavalley 1999).

Experiment 3 assessed whether the vervets could use only associative cues to locate hidden food resources (Table 1). Three platforms were again baited with real bananas and four with sham bananas, all platforms were covered with leaves, and banana skins were placed with sham bananas to remove useable goal-object cues (visual and scent cues). The spatial layout of real and sham rewards was randomized on every trial but a reliable beacon (green plastic boxes) was placed on platforms that contained real rewards (Fig. 2). We hypothesized that if the monkeys used an associative cue to find hidden food, after several training trials, they would learn to associate the green boxes with food and visit platforms with food more often than non-food platforms at levels greater than chance.

Data analyses

During trials, visits to the platforms were scored using all-occurrences sampling. After a certain number of trials in which the monkeys gained experience with the protocol (one or six “learning trials”, see “Results”), the numbers of visits to real and sham sites for each trial and in each experiment were analyzed. Pooled data from multiple individuals were used but since visits were not independent, trials were analyzed separately and combined using repeated *G* tests of goodness-of-fit. Expected values were calculated based on chance levels (i.e., proportion of sites that contained real bananas (3/7) and the proportion that contained shams (4/7) multiplied by the number of visits

for each experiment). In repeated *G* tests, the results of groups of *G* tests can be summed and the overall difference from expected values can be determined for groups of trials within a single experiment (Sokal and Rohlf 1981). This allows the testing of multiple null hypotheses, and can provide information on: (1) whether results from each trial differ from expected (individual *G*-values), (2) whether the relative proportions of data in each category for each trial differ from expected (total *G*-values), (3) whether the pooled data differs from expected (pooled *G*-value), and (4) whether each individual trial is significantly different from one another (heterogeneity *G*-value), which is especially useful for examining the differences between individuals (McDonald 2009). For our purposes, the total *G*-values and pooled *G*-values were of interest and were reported. Percent success for each experiment was calculated as the number of platforms with real rewards visited, divided by the number of total visits, times 100 (Fig. 3).

For Experiments 2A and 2B, results did not differ from chance and it was considered advantageous to determine the strength of the null hypothesis relative to the alternative hypothesis using a Bayesian analysis (Gallistel 2009; Kruschke 2011). The distribution of individual success rates (visitations to real vs. sham sites) during these two experiments were examined with one-sample *t* tests, first



Fig. 2 Feeding platform set up for Experiment 3, with reliable beacon provided

with a theoretical mean of chance ($3/7 = 0.43$) and second, as the alternative hypothesis, with a theoretical mean consisting of the success rate in Experiment 1A (0.60). The Bayes factor (K) was calculated from the ratio of the instantaneous probability of each t -value under the t -distribution for that particular mean. G tests were run using The Handbook for Biological Statistics (<http://udel.edu/~mcdonald/statrepctestof.html>) and t tests were calculated using the Vassar Stats: Website for Statistical Computation (<http://vassarstats.net/>). Significance was set at $P = 0.05$.

Results

Food detection

When provided with global spatial cues, local layout cues and goal-object cues (Experiment 1A), after only a single trial with which to gain experience (a “learning trial”), vervet monkeys were successful 60 % of the time and visited platforms with real bananas more often than those with sham bananas (11 trials, $N = 98$ visits, total $G = 19.60$, $df = 11$, $P = 0.051$, pooled $G = 11.02$, $df = 1$, $P = 0.001$; Table 2; Fig. 3). When the spatial layout of real versus sham rewards was rotated (Experiment 1B), the monkeys again went to platforms containing real bananas more often than those with sham bananas after a single learning trial (11 trials, $N = 67$ visits, total $G = 30.35$, $df = 11$, $P = 0.001$, pooled $G = 22.48$, $df = 1$, $P < 0.0001$; Fig. 3) with a performance of 72 % success (Table 2).

Goal-object cues appeared to be more salient than global spatial cues or local layout cues for vervets. This was indicated by the first two trials of Experiment 1B, when initially, after the spatial layout of real versus sham bananas had been altered, 60 % (3/5) of arriving individuals did not first go to a platform that had previously contained a real banana; rather these new arrivals studied the platforms before going to one that had previously contained a sham banana but now had a real reward. The remaining 40 % (2/5) of arriving individuals went to platforms that had previously contained a real reward. Only one of these individuals acted as though he expected that a real reward would be at that site; this subadult male picked up the sham banana, sniffed it, and banged it against the platform before moving on.

Of the goal-object cues that were available to the monkeys, visual cues appeared to be the dominant means with which vervets located real bananas. An indication that visual cues were used more than olfactory cues were the initial reactions of individuals to the styrofoam bananas. During the first three trials of Experiment 1A, when the monkeys were first exposed to the sham bananas, they visited sham sites as often as real sites (3 trials, $N = 39$ visits, total $G = 5.78$, $df = 3$, $P = 0.123$, pooled $G = 1.85$, $df = 1$, $P = 0.174$) and often behaved as though they thought the sham bananas were real.

In Experiment 2A, when goal-object cues were removed and only global spatial and local layout cues provided information for the locations of real rewards (Table 1), the vervets seemed unable to quickly navigate to food. After a single learning trial, performance was 48 % over the next

Table 2 Cumulative observed (O) platform choices by vervets in each experiment in their first, second, and third choices relative to expected values (E)

Experiment		0/1 ^a	1/1	0/2	1/2	2/2	0/3	1/3	2/3	3/3	Performance ^b	Pooled G - for trials	N (trials)	N (visits)
1A: global spatial, local layout and goal-object cues	O	4	7	0	5	6	0	1	5	5	59/98 = 60 %	$G = 11.02$	11	98
	E	6.3	4.7	3.1	6.3	1.5	1.3	4.7	3.8	0.3	42/98 = 43 %	$P = 0.001^*$		
1B: global spatial, local layout and goal-object cues	O	3	8	0	4	7	0	1	6	4	48/67 = 72 %	$G = 22.48$	11	67
	E	6.3	4.7	3.1	6.3	1.5	1.3	4.7	3.8	0.3	29/67 = 43 %	$P < 0.0001^*$		
2A: global spatial and local layout cues	O	6	5	1	7	3	0	4	4	3	40/83 = 48 %	$G = 0.91$	11	83
	E	6.3	4.7	3.1	6.3	1.5	1.3	4.7	3.8	0.3	36/83 = 43 %	$P = 0.341$		
2B: global spatial and local layout cues	O	5	6	1	9	1	0	3	8	0	46/101 = 46 %	$G = 0.27$	11	101
	E	6.3	4.7	3.1	6.3	1.5	1.3	4.7	3.8	0.3	43/101 = 43 %	$P = 0.606$		
3: associative cue	O	10	19	4	18	7	0	10	5	6	151/279 = 54 %	$G = 13.9$	29	106
	E	16.6	12.4	8.3	16.5	4.1	3.3	12.5	9.9	0.8	119/279 = 43 %	$P = 0.0002^*$		

Expected values calculated based on the probability of choosing correctly depending on earlier platform choices

* Significant results

^a Platforms containing rewards over number of platform choices (e.g., 3/3—3 platforms contained rewards on first three choices)

^b Performance calculated as number visits to platforms containing a reward over total platform visits after one training trial

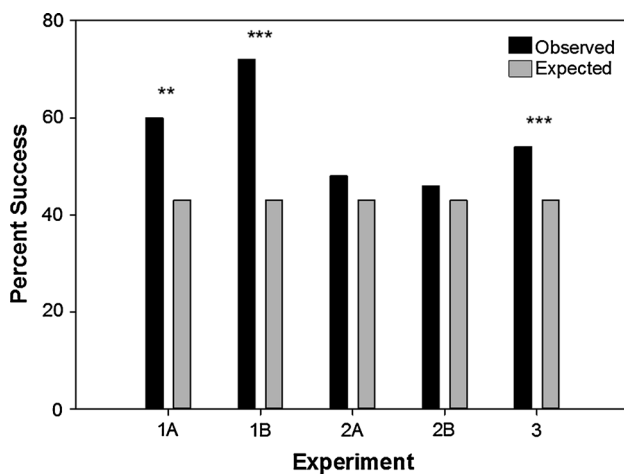


Fig. 3 Percent success in performance observed for each experiment relative to that expected by chance. Significant results indicated by $**P = 0.001$ and $***P \leq 0.0002$

11 trials and they visited sites with sham bananas as often as they visited platforms with real bananas ($N = 83$ visits, total $G = 4.45$, $df = 11$, $P = 0.954$, pooled $G = 0.91$, $df = 1$, $P = 0.341$; Table 2; Fig. 3). Performance did not really improve after two (48 %) or three learning trials (48.5 %). Even after six learning trials, over which global spatial and local layout cues remained the same, the vervets performance was 45.8 % and they still often went to every platform and checked under the leaves (6 trials, $N = 60$ visits, total $G = 2.03$, $df = 6$, $P = 0.917$, pooled $G = 3.48$, $df = 1$, $P = 0.062$). After the single rotation in spatial layout (Experiment 2B), when global spatial and local layout cues changed from Experiment 2A and goal-object cues were still unavailable, the monkeys performance was 46 % and they again visited real and sham sites at the same frequency after a single learning trial (11 trials, $N = 101$ visits, total $G = 4.91$, $df = 11$, $P = 0.936$, pooled $G = 0.27$, $df = 1$, $P = 0.606$; Table 2). Performance did not improve after two (46.1 %) or three (46.1 %) learning trials. After six learning trials, performance was 49 % and monkeys were still checking under every leaf (6 trials, $N = 51$ visits, total $G = 3.76$, $df = 6$, $P = 0.709$, pooled $G = 0.75$, $df = 1$, $P = 0.387$). Bayesian analysis of individual performance ($N = 6$ individuals) during both Experiments 2A and 2B (after two training trials for each individual in each experiment) found positive support for the null hypothesis of chance performance over an alternative hypothesis of 60 % success ($Pr(0.43) = 0.570$, $Pr(0.60) = 0.068$, $K = 8.429$) (Kass and Raftery 1995). In addition, during the first two trials of Experiment 2B when the spatial layout of real and sham rewards was initially changed, only 40 % (2/5) of newly arriving individuals went to platforms that previously contained real food. While 60 % (3/5) of new arrivals went to sites that had previously contained sham bananas.

Use of associative cues

In the absence of global spatial, local layout, and goal-object cues, but the presence of reliable associative cues to indicate the presence of food (Experiment 3), vervets were found to visit sites with real food 54 % of the time (Fig. 3). After a single learning trial, though all data from each trial did not differ from expected (11 trials, $N = 106$ visits, total $G = 11.72$, $df = 11$, $P = 0.385$), the pooled data showed that real food sites were visited significantly more than sham food sites (pooled $G = 4.96$, $df = 1$, $P = 0.026$). Vervets' abilities to use associative cues to find real food improved with a greater number of trials, but again only for pooled data and not when results from each trial were compared with expected frequencies (29 trials, $N = 279$ visits, total $G = 27.48$, $df = 29$, $P = 0.546$, pooled $G = 13.9$, $df = 1$, $P = 0.0002$; Table 2).

Discussion

When examining the sensory cues that vervet monkeys used to locate food items, our experiments showed that goal-object cues were used more readily than global spatial and/or local layout cues. When all cues were available to the monkeys, they had no problem locating real rewards. However, in Experiment 1B, when a switch in the location of real versus sham rewards was done, most arriving monkeys went to platforms where goal-object cues showed that a real banana was present, rather than going to those that had previously contained real rewards. Of the goal-object cues that were available, the sight of real rewards seemed to be the most salient information for vervets. They did not appear to pay as much attention to olfactory cues. Indeed, when first exposed to the sham bananas (which had previously been kept separate from real bananas and did not smell authentic), the monkeys reacted to them as though they should be real; repeatedly smelling them, biting them, and sometimes taking them away from the platforms and up trees. Biting of the sham bananas led to the total destruction of two of them. The dominance of sight over smell when foraging was not unexpected for vervets given their enhanced visual system and limited olfactory sense (Barton 2006; Jacobs 2009).

Reliance on goal-object cues over the cues to spatial location provided by the global spatial relationship of the platforms in the environment and the local layout of resources on each platform, however, differs for vervets compared with the results of similar studies on New World monkeys (Garber and Dolins 1996; Garber and Lavallee 1999; Bicca-Marques and Garber 2004). For white-faced capuchins (*Cebus capucinus*), Garber and Lavallee (1999)

found that global spatial and local layout cues were largely relied upon when locating food resources, though this study did not differentiate between these distant and more near-to-site types of information. Similarly, Bicca-Marques and Garber (2004) found that night monkeys (*Aotus nigriceps*), emperor tamarins (*S. imperator imperator*), saddle-back tamarins (*S. fuscicollis weddelli*), and titi monkeys (*Callicebus cupreus*) were able to find food when only global spatial and local layout cues were available to them. For moustached tamarins (*Saguinus mystax mystax*) that also found food using spatial cues, the study design used by Garber and Dolins (1996) allowed differentiation of the use of global spatial and local layout cues. The results of these experiments indicated that moustached tamarins primarily used more distal global spatial cues to locate food over the use of local layout cues. In our study with a similar sample size, the poorer performance of vervet monkeys on Experiments 2A and 2B suggested that, in small-scale space, they do not readily use global spatial and/or local layout cues to find food sources. The monkeys' visits to platforms containing real food rewards in Experiment 2A did not reach significance and upon rotation of the location of rewards, most individuals did not return initially to sites that had previously held real food. In Experiment 2B, the vervets again failed to visit platforms with real rewards more than those with sham bananas.

An obvious difference between catarrhine vervet monkeys and the platyrrhines that have been previously tested by Garber and colleagues (Garber and Dolins 1996; Garber and Lavallee 1999; Bicca-Marques and Garber 2004) is the specialization of their visual system. Relative to platyrrhines, catarrhines have an expanded parvocellular pathway, which aids in visual acuity in the central visual field and in color vision (Kaas and Huerta 1988; Isbell 2009). Indeed, trichromatic color vision is ubiquitous in Old World monkeys, but among the New World monkeys examined by Garber and colleagues (Garber and Dolins 1996; Garber and Lavallee 1999; Bicca-Marques and Garber 2004), night (or owl) monkeys are uniformly monochromatic (Jacobs et al. 1996) and capuchins, tamarins, and titi monkeys are polymorphic for this trait, with males being dichromatic and females showing a mix of trichromatic and dichromatic phenotypes (Jacobs 2009). Nevertheless, differences in color vision and visual acuity between catarrhines and platyrrhines seem unlikely to explain why vervets failed to easily locate food resources using global spatial and local layout cues, since spatial tasks are inherently visual.

We suggest that our results do not show with certainty that vervets cannot use spatial information to find food, only that spatial cues may be relatively less important when compared with platyrrhines, and that the smaller effect might require a larger sample size to be revealed. It is

notable that in large-scale space (i.e., the area that cannot be seen entirely from a single vantage point, sensu Byrne 2000), the vervets' knowledge of where in their home range the feeding platforms were located, indicated memory and use of spatial information on a daily basis. The proximal spatial location of food in small-scale space changes more often and is less stable than distal spatial layout, like the location of food trees in a home range (Poucet 1993); therefore, it may be less cognitively costly for vervets to rely heavily on goal-object cues in proximal situations, not committing proximal spatial cues to memory, and to use memory only for stable, distal cues in their environment. The ability of primates to navigate directly to out-of-sight resources in large-scale space has been shown for several species and suggests that spatial memory is important for efficient travel around large home ranges (*Saguinus mystax*, *S. fuscicollis*, Garber 1989; *Cebus apella*, Janson and Di Bitetti 1997; *Pithecia pithecia*, Cunningham and Janson 2007; *Ateles geoffroyi*, Valero and Byrne 2007; *Lophocebus albigena johnstoni*, Janmaat et al. 2006a, b; *Papio ursinus*, Noser and Byrne 2007; *Hylobates lar*, Asensio et al. 2011; *Pan troglodytes*, Normand and Boesch 2009).

The vervet niche may also help explain their strong reliance on goal-object cues, especially vision. Unlike many primates, vervets usually occupy savannah-woodland ecosystems and are found in open areas and along forest edges (Enstam Jaffe and Isbell 2009); thus, they often forage through areas where long-range visual information can be readily used to detect food and predators (Sumner and Mollon 2000). For species residing in closed forests, vision may not be as heavily relied upon because individuals often have their sight blocked by barriers. In more open habitats, animals may become reliant on vision and color vision may aid this adaptation. For instance, in polymorphic marmosets (*Callithrix geoffroyi*), Caine and Mundy (2000) found that trichromats were better than dichromats at detecting food at distances up to 6 m. To our knowledge, food detection by wild primates at ranges greater than 6 m has not been examined relative to their visual system, but species in open areas with color vision may be at a visual advantage.

Though our study did not set out to explicitly test rule-based foraging for vervet monkeys, their failure to find food using only global spatial and/or local layout cues implies that they do not use a win-stay foraging rule. This result is curious considering that this foraging strategy has been found in several primate species and that individuals would have improved foraging success if they were able to predict the location of productive feeding sites (Terborgh 1983; Garber 1989; 2000; Garber and Dolins 1996; Janson 1996). More research is needed before it can be concluded

that vervets cannot use nearby spatial cues to find food and that they do not use a win-stay foraging rule. We make this statement because the results of Experiment 2A ($P = 0.062$) suggest that with a greater sample size, vervets would use a win-stay rule. Certainly, during their natural foraging, vervets often returned to small fruit trees that they previously fed from, indicating that win-stay is used by them in some circumstances. Though our goal here was to replicate earlier studies on platyrrhines, future research should focus on experiments specifically designed to test rule-based foraging and on increasing trial number, perhaps by having multiple feeding stations with the same platform set up, in different areas of the home range. The spatial position of food may also need to stay the same over longer time periods than those tested here (6 days) before vervet monkeys encode this information. Differences between species in the capacity to easily remember food site location may be related to their natural history. For example, Platt et al. (1996) found that the abilities of golden lion tamarins (*Leontopithecus rosalia*) and Wied's marmosets (*Callithrix kuhli*) to use a win-stay rule and remember food location over variable time periods depended upon the time it takes for their resources to renew in natural situations. The tamarins resources were more slowly renewing than those used by the marmosets, which may have been associated with the tamarins' better long-term memory of resource location.

Like many other animals (reviewed in: Spetch and Kelly 2006), vervet monkeys were able to use associative cues to orient themselves and find hidden food resources. The use of an associative cue shows egocentric localization (Burgess 2006) but does not inform us about the navigation strategies or the types of allocentric representations that vervets may be capable of. Future research will expand upon these data and investigate if vervets can also use the relationship between an array of landmarks to accurately find food rewards, a task that would allow it to be determined if they can use an allocentric strategy to navigate (Sutton et al. 2000; MacDonald et al. 1994; Potì et al. 2005; 2010; Marsh et al. 2011).

This study demonstrates that the use of comparable experimental methods with distantly related species can reveal important similarities and differences in their use of spatial information and different sensory modalities. The finding that documented differences often appear to map onto phylogeny and niche indicates that variation is a result of the evolutionary path followed by each species. It also raises intriguing questions concerning the selective pressures that lead to variation in spatial abilities and the reliance on certain sensory modalities over others. The fields of sensory ecology and spatial cognition appear ripe for future research taking a comparative and evolutionary perspective.

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