

Flexible use of spatial cues in the southern flying squirrel (*Glaucomys volans*)

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Abstract Insects, birds, and mammals have been shown capable of encoding spatial information in memory using multiple strategies or frames of reference simultaneously. These strategies include orientation to a goal-specific cue or beacon, to the position of the goal in an array of local landmarks, or to its position in the array of distant landmarks, also known as the global frame of reference. From previous experiments, it appears that birds and mammals that scatter hoard rely primarily on a global frame of reference, but this generalization depends on evidence from only a few species. Here we examined spatial memory in a previously unstudied scatter hoarder, the southern flying squirrel. We dissociated the relative weighting of three potential spatial strategies (beacon, global, or relative array strategy) with three probe tests: transposition of beacon and the rotation or the expansion of the array. The squirrels' choices were consistent with a spatial averaging strategy, where they chose the location dictated by at least two of the three strategies, rather than using a single preferred frame of reference. This adaptive and flexible heuristic has not been previously described in animal orientation studies, yet it may be a common solution to the universal problem of encod-

ing and recalling spatial locations in an ephemeral physical landscape.

Keywords Spatial memory · Navigation · Landmark · Decision · Sciuridae

Introduction

Spatial orientation is not only critical for the organization of adaptive behaviors, such as foraging and reproduction, but also poses important cognitive problems (Jacobs 1995). Perhaps because the cost of being disoriented is high, the birds, mammals, and insects that have been studied to date rely on redundant sensory modalities to orient themselves in space (Berthold 1991; Papi 1992; Wehner et al. 1996). The actual orientation, however, depends not only on the nature of the sensory input, but also the organization of this input into useable frames of reference. Spatial positions may be coded, and subsequently recalled, relative to landmarks, arrays, distributed cues, or in reference to movement (Jacobs and Schenk 2003). Yet, such cues are rarely segregated in the natural environment. A landmark such as a tree has both a spatial location and a position within an array of similar and dissimilar objects. It may also be a rich food source (e.g., a fruiting tree), identifiable by its odor or visual appearance, and therefore may act as a beacon, where the stimulus is coincident with the goal. Finally, an animal may accumulate a movement history from this location to a fixed location such as its nest.

It is therefore important to determine not only what information an animal has for orientation, but how it stores and subsequently retrieves this information. The relative weight given to different frames of reference can be influenced by fixed preferences for a certain hierarchy of cues, as seen in

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species comparisons, or by subtle changes in weighting influenced by changes in cost or reliability of certain cues or sensory inputs. For example, Maaswinkel and Whishaw argued that the laboratory rat (*Rattus norvegicus*) shows a hierarchical preference for visual, olfactory, and self-movement cues, in that order (Maaswinkel and Whishaw 1999). Jacobs and Shiflett reported that free-ranging fox squirrels (*Sciurus niger*) tested on an outdoor maze showed a similar hierarchy, preferentially using distal spatial information, not beacon, local cue grouping, or self-movement strategies (Jacobs and Shiflett 1999). Such hierarchies are not fixed, however, but appear to change with ambient conditions. Laboratory rats trained in dim light, on a radial arm maze with odor cues at each arm, learn the explicit spatial configuration of the odors. When the room is fully illuminated, however, the rat's use of odor information is influenced by the visual cues (Lavenex and Schenk 1996). Likewise, free-flying rufous hummingbirds (*Selasphorus rufus*) orient to the relative position of a target in an array of closely-spaced artificial flowers, but switch to a global position strategy if the array components are dispersed more than 40 cm apart (Healy and Hurly 1998). Although this body of work has traditionally been interpreted as evidence for hierarchy of cue use, Cheng has argued for an important alternative view, according to which information from several cues is averaged rather than single cues being used in a strict hierarchy (Cheng 1995, 2005; Cheng and Spetch 1998; Cheng and Gallistel 2005).

Even within a modality, such as vision, cues may be distal or local. This distinction has been proposed to determine which frame of reference they contribute to, and even to the construction of the underlying spatial representation by the hippocampus, in the case of birds and mammals (Jacobs 2003). For example, Brodbeck (1994) showed that black-capped chickadees (*Poecile atricapillus*) use spatial information hierarchically during the retrieval phase of spatial memory tasks. Chickadees preferentially oriented to a global frame of reference, then to the site's relative location within an array of feeders, and only lastly to the unique color and pattern of the remembered feeder. In contrast, the dark-eyed junco (*Junco hyemalis*), also recalled the feeder by these three strategies (global, relative, beacon), but showed no consistent preference for one strategy over another (Brodbeck 1994). This same distinction of the scatter hoarding species preferring a global orientation strategy was also demonstrated in a comparison within pairs of European parid and jay species (Clayton and Krebs 1994).

The evidence that scatter hoarders use a distinctive strategy, however, still comes from relatively few species and it is important to extend this number to test its generality—preferably by including species whose use of space poses different cognitive problems from those faced by species



Fig. 1 Photograph of experimental subject eating a block of mouse chow outside his cage, photograph by Anna Waisman

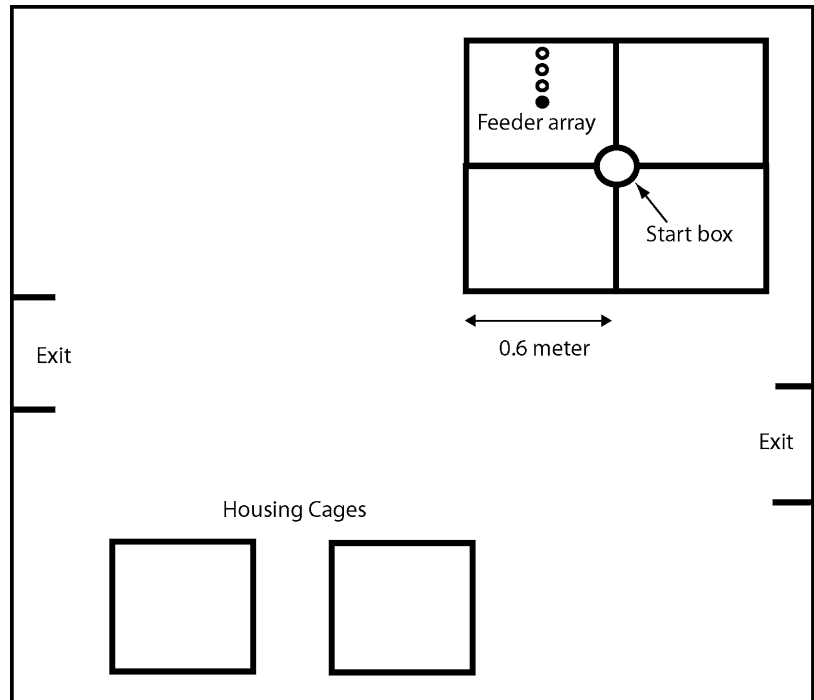
that have already been studied. The southern flying squirrel is an unusual food-storing species in this regard (see Fig. 1). Most obviously, flying squirrels move in three-dimensional space in a way unlike any other rodent whose spatial memory has been studied: controlled gliding flight (Essner 2002). They store food, however, in a two-dimensional space; like the gray (*S. carolinensis*) and fox squirrels with whom they compete for food, they collect tree seeds such as oak acorns and hickory nuts in the canopy of the eastern deciduous forest. All three squirrel species then travel to the ground to bury nuts individually in widely distributed scatter hoards in the forest litter (Wells-Gosling 1985). But unlike the gray and fox squirrels, flying squirrels are the only mammalian species to use gliding flight to scatter hoard each seed that they cache. Among sciurids, flying squirrels are also secondarily nocturnal (Mercer and Roth 2003). They therefore must encode their two-dimensional map of cache locations in conditions more similar to those faced by the scatter-hoarding Merriam's kangaroo rat (*Dipodomys merriami*), whose recall of cache locations is strongly influenced by the presence of local landmarks (Barkley and Jacobs 1998).

Materials and methods

Rationale

To address the question of spatial encoding in flying squirrels, we began with a simple paradigm to determine which

Fig. 2 Overhead view of the arena floor during training. The start box is shown at the arena center. The array is pictured in the upper left quadrant, with the black circle indicating the baited cup and open circles indicating empty cups



spatial frame of reference would be used by a flying squirrel to return to a single remembered location on the ground. We trained squirrels to return to one of the four feeders, arranged in a line (Fig. 2). We predicted that the squirrels would encode the location using one or more of the three strategies: in reference to the absolute location of the reward in the room (global strategy); in reference to the reward's position in the array of four objects (relative strategy); or by directly orienting to a visually-distinctive stimulus associated with the reward (beacon strategy). To determine which strategy the squirrels used, we performed three unbaited probe tests, where the array was either rotated, expanded, or rearranged (i.e., the distinctive cue was transposed to an alternate object and hence, alternate position in the array). The use of each strategy leads to distinct predictions of how the squirrels would behave in each probe. To avoid any possibility of learning, we gave only one probe test of each type to each squirrel. In spite of the multiple possibilities for error on each trial, the design nonetheless had adequate power to detect deviations from each strategy.

Subjects

The subjects were five male captive-bred southern flying squirrels (two years old), individually housed on a 12:12 (light:dark) cycle and maintained at 95% of pre-test body weight on a diet of fresh vegetables, mixed nuts, and *ad libitum* access to water. Prior to testing, squirrels were placed on 18 h of food restriction to a fresh vegetable diet with *ad libitum* access to water.

Apparatus

The squirrels in this study were housed in the same square (3.25 m × 3.45 m) room used for testing. The room contained several fixed landmarks, including the arena (described below), two facing doors (painted in a contrasting color to the walls), and the cage rack. The room was brightly illuminated during their inactive period (12 h/day) and all squirrels were allowed to freely explore the room during housing changes. For training and testing, squirrels were moved across the room from their home cages to the test arena, held in a translucent plastic funnel. The squirrels therefore were trained and tested in a novel arena located in a familiar room.

The testing arena was a tall square arena (1.2 m × 1.2 m × 1.9 m high), consisting of a clear acrylic box, framed in painted wood, mounted on castors (13 cm elevation from floor) with a wood-framed door occupying one entire wall. The arena floor was made of four square wood tiles (Masonite™), painted white, that could be cleaned and interchanged among trials to eliminate odor cues. Illumination was provided by one overhead 25 W red bulb to produce a level of illumination typical of the squirrels' natural environment during their active period.

One quadrant of the arena contained an array of four objects. Each object was constructed from a black plastic cylinder (film canister, 3 cm diameter × 5 cm high) mounted on a black rubber stopper (cage water bottle stoppers, 2.5 cm diameter × 3 cm high). This linear array was produced by arranging the objects so that one was centered on one of

the four floor tiles and the remainder were in a linear array with centers 3.9 cm apart (Fig. 2). All objects were fixed to the floor tile. One object within the array (the beacon) was marked with a black and white striped plastic disk (2.5 cm diameter, commercial button) affixed to the cylinder. A round, transparent acrylic cylinder (30 cm diameter) was used as a start box.

Procedures

Pretraining

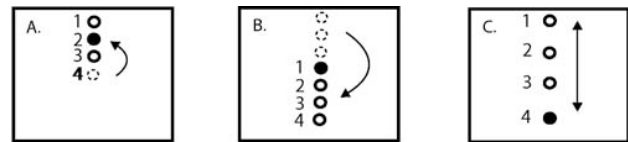
Squirrels were given three 15-min habituation trials to explore the empty arena before they were shaped to the task. Following habituation, squirrels were shaped to find food in the objects by removing the small plastic cylinder covering the food reward (0.2 g shelled pecan) hidden inside. This was accomplished gradually in successive trials where the food reward was placed further under the object until squirrels correctly removed the object from the stopper and ate the food reward on three consecutive trials.

Training

Following pretraining, the stimulus array was set up in a different quadrant of the arena, and the arena was relocated within the test room to reduce any carry-over effects from the relative and global position of the array during shaping. The training array consisted of four identical objects. To eliminate odor cues, no squirrel had previous contact with any of these training array objects. During training trials, the subject was first placed in the start box for 10 s. The target object (i.e., the cylinder with the button) was always at the end of the array furthest from the arena wall, and was always baited during training with the pecan placed under the cylinder and out of sight of the subject. Floor tiles were swept and shuffled between all trials, and cloths saturated with alcohol were used on the array and all arena surfaces to eliminate other odor trails. Up to 20 training trials were given per day. Training for each squirrel ended when it had performed three consecutive correct training trials.

Testing

Each testing block consisted of two standard baited trials and one unbaited probe trial, followed by further standard trials until two consecutive correct choices were made. Thus, there were at least five trials per block. There were three types of probe trials: transposition, rotation, expansion (Fig. 3). Each test occurred only on the middle trial of the block, and each subject was only given one trial for each type of probe test. The order of probe tests was counterbalanced across individuals. The probe tests were unbaited to eliminate odor



Manipulation	Strategy Predictions			Results
	Beacon	Array	Global	
A. Displacement	Feeder 2	Feeder 4	Feeder 4	Feeder 4
B. Rotation	Feeder 1	Feeder 4	Feeder 1	Feeder 1
C. Expansion	Feeder 4	Feeder 4	Feeder 3	Feeder 4

Fig. 3 Comparison of strategy predictions with results from each of the manipulations. *Shaded panels* highlight consistency between the predictions of several models and the observed results. Cup numbers refer to the illustration panel. *Black circles* indicate the beacon location

cues and to avoid rewarding squirrels for novel responses. To avoid learning effects, each animal was tested on each probe condition once only. All three testing blocks were presented in a single day.

Beacon Transposition

The distinctive cue (i.e., the button) was moved to another object in the array (from the object furthest from the arena wall to the object next but one to the wall). Squirrels using global and relative strategies should search at the prior location, while squirrels using a beacon strategy should search at the new beacon location (Fig. 3).

Array Rotation

A 180° rotation of objects around the baited object produced a mirror-reversed array relative to training conditions. This manipulation dissociated two of the three strategies as illustrated in Fig. 3: squirrels using the relative strategy should search at the new endpoint of the array, while squirrels using the beacon strategy or the global strategy should search at the button-marked object.

Array Expansion

The distance between objects was doubled while preserving their relative positions (Fig. 3). Beacon and array-based coding predicts an initial search at the beacon location, while global coding predicts a search at an intermediate cup corresponding to the previous location of the rewarded cup in global (i.e., room) coordinates.

Analysis

Before examining the predictions of the different strategies for cue location, it was first necessary to establish that behav-

ior on the probe trials was nonrandom. The null hypothesis is that the probability of going to each location is 1 of 4, or 0.25. Because of the limited number of subjects, chi-squared or G-tests could not be used to test whether the distribution of choices differs from this pattern. Instead, the exact probabilities of the observed distributions of the squirrels' choices on the null hypothesis, and of more extreme distributions, were calculated using the multinomial distribution for each of the three tests.

If behavior in probe tests is nonrandom, the predictions from the three strategies (global, relative, beacon) can then be tested, also using exact multinomial tests. As Fig. 3 shows, in each probe test, two of the strategies predict the same behavior. Hence in a single test, a squirrel might be choosing one strategy or choosing the solution converged upon by more than one strategy. The key question about each strategy, therefore, is whether it correctly predicts behavior in all three probe trials. These tests require an estimate of the probability of correct response on a probe trial, if a squirrel was accurately following a cue. This estimate was obtained from the standard trials that were given in test blocks.

Results

The squirrels reached the training criterion in a mean (\pm SE) of 29.4 (\pm 0.5) trials. During the test blocks, three squirrels made one error each on one of the standard trials following one of the probe tests. In all other standard trials within the test blocks, the squirrels correctly chose the baited object. Treating the animals as a group, the total number of standard trials given within test blocks was 63. The probability of a correct response in such a trial was therefore 60/63.

The squirrels made rapid choices on unbaited probe trials, implying that the pecan odor was not a primary source of orientation information. In all three probe tests, four of the five squirrels made the same choice. The fifth squirrel made a unique choice on the transposition and the expansion tests, but the same choice as the others on the rotation test.

As summarized in Fig. 3 and illustrated in Fig. 4, the squirrels' choices during probe tests were nonrandom, and the deviation from the random distribution was significant (summed $\chi^2 = 22.18$, $df = 6$, $p = 0.0011$, method of Jones and Fiske 1953). We therefore examined evidence for or against the other spatial strategies.

Beacon hypothesis

According to the beacon strategy, the squirrels will identify the unique object as the training location. The squirrels' behavior was almost exactly consistent with this hypothesis in the rotation and expansion tests. However, their behavior deviated from this prediction in the transposition test.

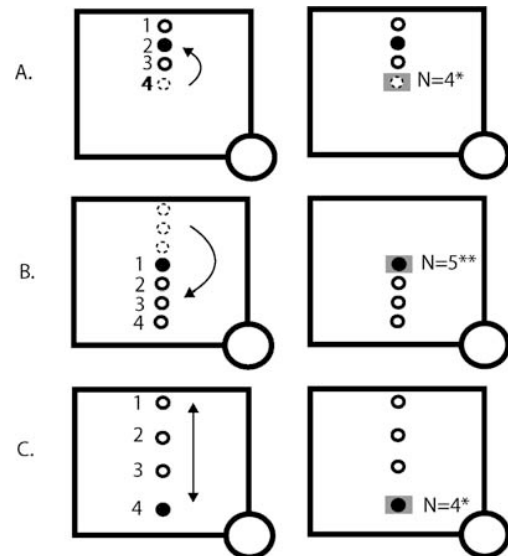


Fig. 4 Summary of manipulations and results. In the left column, arrows show changes to the array from the training condition. In the right column, shaded boxes show the animals' search choice. All choices are significant ($p < 0.05$). The black circle indicates the location of the beacon cue. No bait was placed during the manipulations

In this test, the observed frequencies of choice of the four cylinders were 0, 1, 0, and 4. The deviation from the Beacon prediction was significant. According to the Beacon hypothesis, the squirrels' probability of going to the location containing the marked object in the probe tests should be the same as their probability of correct response on standard trials within test blocks, i.e., 60/63. Their probability of going to each of the nontraining locations should therefore be 1/63 (one-third of the remaining probability). An exact multinomial test shows that the significance of the deviation of the observed frequencies from this predicted pattern is less than 0.00001. Even if the significance level is deflated (Jones and Fiske 1953) to allow for the fact that behavior was almost exactly as predicted from the beacon hypothesis in the rotation and expansion tests, it remains equal to 0.0001. Therefore, we can reject the beacon strategy as an explanation of the data from the three probes taken together.

Global location hypothesis

According to this hypothesis, the squirrels will identify as the training stimulus whatever object is in or nearest the absolute training location. Behavior in the rotation and transposition tests was consistent with this prediction, but in the expansion test it was not. In this test, two locations were equidistant from the training location. The probabilities of going to the four locations according to the global location hypothesis can therefore be taken as 3/126, 30/63, 30/63, and 3/126. The corresponding observed frequencies were 0, 0, 1, and

4. The exact multinomial test shows that the significance of the deviation from the predicted pattern is less than 0.00001. Deflated to allow for the fact that behavior in the rotation and expansion tests was almost exactly as predicted by the global location hypothesis, the significance level remains at 0.0003. Therefore, we can reject the global location hypothesis as an explanation of the data from the three probes taken together.

Relative location hypothesis

According to the relative location hypothesis, the squirrels will identify the “last position in the array” as the training position, with a probability of 60/63 of using this rule in each of the three probe tests. In the transposition and expansion tests, the squirrels’ behavior was largely consistent with this hypothesis. But in the rotation test, their behavior deviated from the prediction. The observed frequencies of choice of the four cylinders were 5, 0, 0, and 0, compared with predicted probabilities of 1/63, 1/63, 1/63, and 60/63. An exact multinomial test shows that the significance of the deviation from the predicted pattern is less than 0.00001, and remains so even when deflated to allow for the fact that behavior in the transposition and expansion tests was almost exactly as predicted from the relative location hypothesis. Therefore, we can reject the relative location hypothesis as an explanation of the data from the three probes taken together.

Discussion

Previous experiments have found that scatter-hoarding species tend to use global frames of reference, when orienting to a remembered location (e.g. Brodbeck 1994; Clayton and Krebs 1994). However, in the present study of strategy use by the southern flying squirrel, we found that the animals did not use such a fixed hierarchy of cues. While their recall strategy was clearly nonrandom, no single (or pure) spatial strategy could describe behavior in all three probe trials, and in particular, the global frame of reference was not always preferred. Our results are therefore consistent with a spatial averaging model of the kind favored by Cheng (e.g. Cheng 1995, 2005).

In the expansion test, primary use of global cues would predict that squirrels return to the correct cylinder in room-based coordinates, regardless of that object’s position within the array. Instead, subjects chose the cylinder consistent with both the beacon and the array-based cues. Likewise, in the transposition test, using only the nonrelational beacon strategy would predict a search at the new position occupied by the beacon. Instead, subjects chose the cylinder predicted by the conjunction of global and array-based cues. Finally, the outcomes of both the beacon transposition and the expansion manipulations are consistent with the use of array-based rep-

resentations of the target location. However, the squirrels did not use an array-based strategy on the rotation test. The subjects instead chose the object predicted by the conjunction of global cues and the beacon, and not by the object’s relative position within the array (Fig. 4).

If the squirrels had used a fixed hierarchy of cues, the preferred cue would have predicted response in all probes, since all cues were available on all trials. In addition, the probes were never repeated, and so the squirrels did not have the opportunity to learn that a cue had been devalued. In fact, however, no single cue successfully predicted the results of all the three probes. Instead, the squirrels’ behavior was consistent with the hypothesis that when different strategies indicated conflicting responses, they made the response that was consistent with most of the strategies. A possible alternative explanation is that the squirrels were not able to see landmarks sufficiently well to make use of the extra-arena cues. The squirrels in this study, however, were tested in their familiar housing room, with its familiar landmarks, all of which were illuminated 12 h per day. We therefore think it unlikely that their performance was related to a lack of information about the space in which they were tested. It is possible that the clear acrylic of the arena distorted their perception of the external cues. However, laboratory rats can maintain their location relative to their home cage, while being transported between test rooms (White and McDonald 1993); in this case the squirrels were transported only a meter. Finally, for squirrels to use more than one strategy assumes that they possess the requisite information for each strategy. Their lack of dependence on a pure global strategy therefore seems unlikely due to lack of information about global position, particularly in light of their exploratory experience, and the fixed relationship between home and test arena.

It can instead be assumed that the cues that underlie different frames of reference (global, relative, or beacon) are accorded different weights in the averaging process, and a hierarchy is what would emerge if there are marked disparities between the weights accorded to different cues. What might determine the weights assigned to different cues? An obvious possibility is the reliability of a cue within the experimental situation, as has been demonstrated in studies with laboratory rats (Biegler and Morris 1996; Pearce et al. 2000). Yet in our study, when the beacon predicted the reward location 100% during training and > 80% during testing, the squirrels appeared to weigh and utilize other strategies when these were advantageous. Their behavior thus appears to rule out a strategy based on the reward probabilities of the beacon experienced during training and most test trials. Instead, the presence of any two convergent strategies overrode any beacon preference, or for that matter, any preference for the use of a single frame of reference.

While this particular result is unique, compromising between conflicting cues or frames of reference is often de-

scribed in spatial orientation studies. For example, in a test of Cheng's vector sum model, pigeons average components of vectors from a landmark to the goal (Cheng 1994). Studies of orientation to two landmarks in Clark's nutcrackers suggests their strategy, like that of the rufous hummingbird, switches at critical deviations from the training condition (Kamil and Jones 2000). Because our squirrels, like the chickadees studied by Brodbeck (1994), had to choose between discrete sites, we could not measure such 'compromises' in their search patterns; instead, we detected an 'averaging' in their discrete choices. In conclusion, such averaging appears to be the most parsimonious explanation of data from three disparate taxa—the goldfish (Vargas et al. 2004; Cheng 2005), the laboratory pigeon (Cheng 1995), and the southern flying squirrel. With future work on more species, we may find that the spatial averaging of cues is the general rule in the recall of spatial locations by mobile animals.

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