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The Spatial Memory of African Elephants (*Loxodonta africana*): Durability, Interference, and Response Biases

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Women and elephants never forget an injury.
—Saki (H. H. Munro), "Reginald on besetting sins," in *Reginald* (1904)

I am not sure whether the satirist H. H. Munro believed Saki's claim, although it may well be true (at least with regard to elephants). This chapter will examine some characteristics of elephant memory more systematically than did Saki.

In general, it is to an animal's advantage to remember some aspects (usually the stable features) of a situation for long periods and to remember other aspects (usually the unstable features) only temporarily. Consistent with recent arguments questioning the value of cognitive constructs for studying animal behavior (Grau 2002; Staddon 2001a,b; Wright and Watkins 1987), I will use "reference memory" and "working memory" (Baddeley and Hitch 1974; Honig 1978) only as descriptive terms indicating formal task requirements. (See Olton, Becker, and Handelmann 1979.) The stable characteristics of the test situation (such as the shape of the spatial array of food sources) are said to involve reference memory; those features that vary across trials (such as the sequence of food sites visited on a trial) are said to involve working memory. My main goal is to demonstrate that elephants can remember which locations they have visited during a spatial memory test similar to the "radial maze" (Olton and Samuelson 1976). The data will show that elephants rely on memory to solve several spatial problems, rather than relying on their response biases (Dale and Innis 1986) or their excellent olfactory abilities (Rasmussen and Krishnamurthy 2000). In addition, I will describe research showing that performance on the memory task is susceptible to proactive interference and that the retention of reference memory components of the test procedures is durable.

Historical Context

Despite the long history of study and management of both Asian elephants (*Elephas maximus*) and African elephants (*Loxodonta africana*), relatively few studies have been conducted to evaluate their memory abilities (Grzimek 1944; Hediger 1955; Hobhouse 1901; Markowitz, Schmidt, Nadal, and Squier 1975; Rensch 1957).

An analog of the radial maze (Olton and Samuelson 1976) was used to examine the spatial memory of African elephants: In particular, their ability to distinguish locations they had visited during a trial from locations they had not visited. Radial-maze and similar tests have been used to study spatial memory in numerous species. These include honeybees (Brown and Demas 1994), fish (Hughes and Blight 1999), birds (Gould-Beierle 2000), mice (Dale and Bedard 1984), rats (Olton and Samuelson 1976), monkeys (MacDonald and Wilkie 1990), great apes (MacDonald 1994), and humans (Dale 1987). As far as I know, the animals most closely related to elephants (manatees and hyraxes; Shoshani 2000) have not participated in spatial memory tests. However, some of the elephant's closest evolutionary "cousins" (Colbert, Morales, and Minkoff 2001), the odd-toed ungulates, have done so (e.g., horses, Marinier and Alexander 1994; Waring 2002). In addition, many of the more distantly related even-toed ungulates have been tested, including cattle (Bailey, Rittenhouse, Hart, and Richards 1989), goats and sheep (Hosoi, Swift, Rittenhouse, and Richards 1995), and pigs (Mendl, Laughlin and Hitchcock 1997). The present studies extend such tests to another large herbivore, the African elephant (*Loxodonta africana*), a large-brained, long-lived species with a complex social structure and a large home range (Moss and Poole 1983).

Basic Characteristics of Elephant Spatial Memory

The elephants were exposed to a series of progressively more complex test situations to provide a preliminary description of this species' spatial memory abilities. After familiarization with an (empty) food container, a large pot, the subjects were presented with a variety of two-pot tests (Dale, Shyan, and Hagan 1994a). In the first two procedures, choices were not differentially rewarded with food (a "spontaneous alternation" task: Richman, Dember, and Kim 1986). At first, the pots at both locations were empty; in later tests, both of the pots were baited (and refilled between choices). Rats typically alternate choices when no food is involved (as do many other animals), but are more likely to repeat choices ("win-stay;" Richman, et al. 1986) when food is available at both locations. The elephants next received a test where alternation (a "win-shift" strategy; Olton and Schlosberg 1978) was selectively rewarded. The two pots were baited at the start of each two-choice test, but the first pot selected was not re-baited between choices. After the two-choice phase, the subjects were tested with arrays of four, and then eight, food locations. The sequence of choices made during these tests was analyzed to identify response patterns and possible algorithms (Dale and Innis 1986; Yoerg and Kamil 1982) being used by the subjects. In addition, several types of olfactory control tests were administered to eliminate the obvious possibility that the elephants might locate the food by smell (Rasmussen and Krishnamurthy 2000).

General Methods

Subjects

The subjects were five unrelated wild-born female African elephants (*Loxodonta africana*) residing at the Indianapolis Zoo. The animals were maintained on *ad libitum* food and water, except during the test. Their diet consisted of hay, fruit, vegetables, browse, and commercial elephant food and vitamin supplements. The subjects were Cita, 23 years old when testing began, approximate weight 3,450 kilograms; Ivory, 10 years old, 2,150 kg; Kubwa, 16 years old, 2,650 kg; Sophi, 24 years old, 4,350 kg; and Tombi, 15 years old, 2,450 kg. They were managed with a "free contact" technique: The animals participated in a variety of activities each day under the direct supervision of professional handlers (zoo staff). The elephants were housed overnight in three stalls in a large barn. On most days, the subjects were released into a large public exhibit near the barn. On cold days (defined by air temperature, humidity, wind speed, and amount of direct sunlight), the elephants stayed in the barn.

Test Environments

The elephants were given the two-pot tests and the initial four-pot tests inside the largest stall in the barn (with only the test animal in the stall). The stall was 8.3 meters by 7.3 meters, with a concrete floor. It was surrounded on two sides by bars and on two sides by concrete walls. There was a wide variety of visual cues available in the barn. A subject started each test standing with its head above a 0.7 meter by 0.5 meter rubber mat, which served to mark the "start" position. The food was contained in 12-quart stainless steel stockpots with tight-fitting lids. Each lid had a small stainless steel handle, which the elephants used to lift the lids. During tests, each pot was placed on a gray plastic pan, 36 centimeters in diameter, with a rim 6 centimeters high. Black marks on the floor under the plastic pans indicated the goal locations for resetting the pots after the elephants had handled them.

The later four-pot testing, and all of the eight-pot testing, was conducted in a fenced arena, approximately 34 meters by 17 meters, outside of the barn. During testing, this arena was divided in half by a yellow rope hanging at a height of 0.5–1.5 meter, designating a 20 meter × 17 meter test area. The start mat and pots/pans were removed between sessions. The test array was replaced before each test, using fence landmarks to place the start mat, and a large "protractor" and ropes to place the pots at 45° intervals relative to the mat. The absolute positions of the test arrays typically varied by less than a meter across days.

The food reward was one food pellet per pot on the two-pot tests, either one or four food pellets on the four-pot tests (Purina monkey chow #5045, approximately 7.3 grams per pellet), and one Red Delicious apple per pot for the eight-pot tests (approximately 130 grams per apple).

Handling Procedures

The elephants were always tested under the supervision of a handler, at least two handlers were present for each test, and the experimenter/observer manipulated the apparatus but did not interact with the elephants. Each animal was on about five days per week. Since the test procedures were novel, the testing schedule was conservative: It was deemed better to give too many trials on a given procedure than to change procedures prematurely.

Data Analysis

Although the observer recorded the subjects' choices during each test, all trials were videotaped for later analysis. During the four-pot tests, the elephants were tested in an "arc array," with the pots close together in a large stall. The subjects sometimes moved quickly in the confined situation, swinging their trunks near more than one pot during a single choice opportunity. It was difficult for either the observer or the handler to be sure how close an elephant's trunk came to the pots during these choices. In addition, subjects occasionally turned away from a pot without touching the lid, but after moving the trunk to within several centimeters of the pot (or touching it). This happened for both baited and unbaited pots. To reduce the possibility that the subjects were using smell to detect food in the baited pots, the criterion for a choice was conservative: Any approach to within a foot (0.3 meter) of a pot constituted a choice, whether the subject touched the pot or not. A few tests were discarded because a subject selected two pots during the same choice opportunity (a "double choice"), even though the animal may have touched only one (or none) of the pots.

Inter-Observer Reliability

Two trained raters evaluated each videotaped trial, comparing scores using Cohen's Kappa coefficient of agreement (Cohen 1960). This measure describes the proportion of agreements in two raters' observations, corrected for the proportion of agreements expected by chance. For each scoring disagreement between raters, the videotape was re-evaluated by the author, who assigned a value to the disputed observation. A few disagreements were the result of one rater assigning the wrong code to an observation. However, most disagreements resulted from trials on which a double choice may have occurred. The data from such "double choice" trials would have been difficult to interpret, and were not analyzed.

Two-Pot Tests: Assessing Response Biases

Before testing proper began, each of the elephants was familiarized with the stockpot during 4–16 brief exposures to a single empty pot in the large stall. Each exposure ended when the elephant touched the pot or after one minute.

No-Food Test

The key question for this test was whether, during its second choice, the elephant would return to the first pot it had touched or choose the other pot. Each elephant was tested in the large stall with two empty stockpots placed

5 meters apart on the floor, and 4 meters in front of the start mat (figure 7.1). The animal was "released" by a handler's verbal cue and allowed 2 minutes to touch one of the pots. The animal was then recalled to the start position and released again. As a procedural control to disrupt potential body-orientation strategies, the elephant was turned around 180°, to face away from the pots, between choices. To eliminate the possibility of unconscious cueing (the Clever Hans effect), different handlers supervised the first and second choices, and the handlers did not watch each other's part of the test. Each elephant except Kubwa was tested until it had completed both choices on 10 trials (Kubwa stopped responding after a few trials). Because, occasionally, an elephant moved the first pot it touched, leaving mucus on the pot's lid, the observer wiped and replaced the lid of the chosen pot, resetting it in its original position. The observer then touched the other pot, wiping mucus on its lid. These control procedures were used for Tombi starting with the two-pot, "replace-food" condition, and for all testing with the other elephants. On each of the two-pot procedures, subjects were tested twice a day, with 3–4 minutes between trials.

In this condition, the elephants frequently failed to complete a choice in under two minutes. The reluctance to choose was particularly evident for Kubwa: this subject completed only two trials under the procedure. Overall, the subjects failed to complete 31 trials. They made "double choices" on two other trials.

As a group, the four subjects which completed 10 trials exhibited a position preference, choosing the pot to their right on 75 percent of their initial choices during a trial, $t(3) = 5.0$, $p < 0.05$ (table 7.1). The tendency for "spontaneous alternation" was evaluated using a correction for initial response biases (Dember and Fowler 1958): Expected proportion of alternations, $E(\mathrm{alt}) = [1 - (p_L^2 + p_R^2)]$, where p_L = the proportion of initial choices to the left and p_R = the proportion of initial choices to the right. Using the left/right response bias on the first choice of completed trials (table 7.1), an expected alternation frequency was calculated. For example, Cita chose the pot on the right on 8/10 initial choices, producing an expected alternation rate of 0.32. The difference between the actual alternation frequency and the expected alternation frequency was calculated for each subject completing 10 trials. The mean difference score for these four subjects (3.15) was statistically significant, $t(3) = 6.68$, $p < 0.01$, suggesting a tendency to alternate choices in this situation. (Without using the correc-

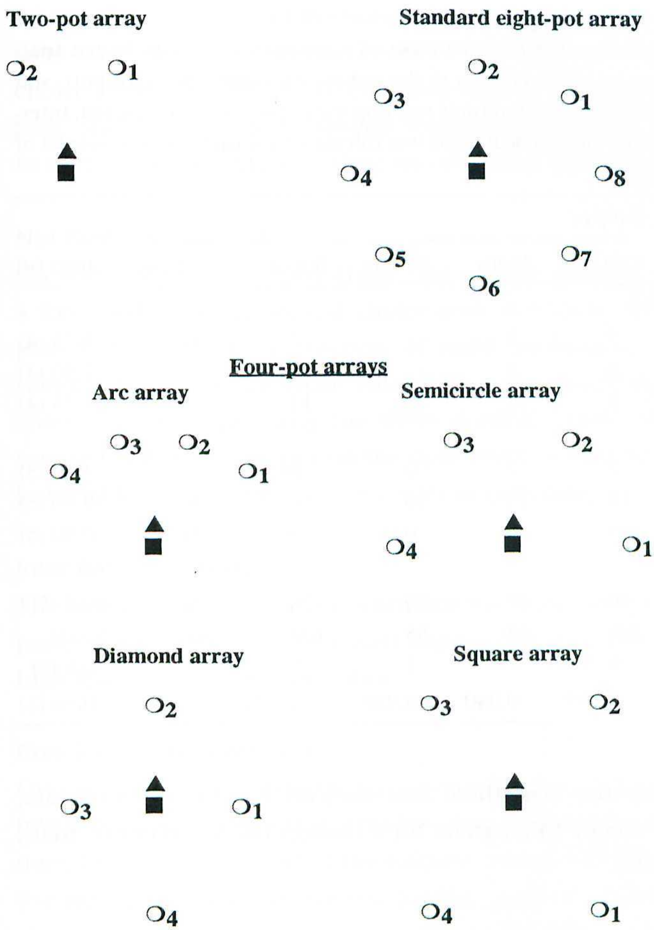

Figure 7.1
The two-pot, four-pot, and eight-pot arrays used in the series of memory tests. The pot locations are numbered as they were for data collection. The diagrams indicate the relative locations of the pots (open circles), the elephant's starting position over the mat (filled square) and the elephant's orientation when released to make a choice (filled triangle). The eight-pot array was rotated 22.5° on some of the later tests, putting four pots in front of the subject and four pots behind it.

Table 7.1
Choice patterns on the two-pot tests. Number of response alternations in ten trials (alternations), number of initial choices to the pot on the right side (right pot), and number of trials discarded before ten trials meeting the criteria were completed. Inter-rater reliability (Cohen's Kappa coefficient) was calculated for each subject over all of the two-pot conditions.

Condition	Subject					
Measure	Cita	Ivory	Kubwa	Sophi	Tombi	Mean (*n*)
No food						
Alternations	7	5	—	7	8	6.75 (4)
Right pot	8	8	—	8	6	7.50 (4)
Discarded	8	3	6	13	3	6.75 (4)
Replace food						
Alternations	7	2	0	0	7	3.20 (5)
Right Pot	10	10	10	10	9	9.80 (5)
Discarded	0	0	0	0	0	0.00 (5)
Not replace food						
Criterion	10	22	20	28	18	19.6 (5)
Right pot (%)	100	48	85	100	83	83 (5)
Discarded	0	1	1	1	1	0.6 (5)
Cohen's Kappa	1.000	0.940	0.950	0.950	0.950	0.96 (5)

tion for initial response bias, these four subjects had only a moderate, non-significant tendency to alternate their choices (67.5 percent of trials; $t(3) = 2.38$, $p > 0.05$).

Replace-Food Test

Before this test, each elephant was given 10–30 opportunities to collect a single food pellet from a closed pot placed on the floor below the animal's head. After this training, all five elephants collected the food pellet rapidly.

In the replace-food test, a food pellet was placed in each pot to see whether adding food would influence the animals' search strategies (Richman et al. 1986). The pot opened on the first choice was re-baited before the elephant's second choice, and both pots were touched and reset by the observer. Each subject received 10–12 trials on this task.

Once food was available in each pot, every subject completed every trial. The initial response bias was even stronger, with the pot to the right being selected on 98 percent of the initial choices (table 7.1). Each of the five subjects exhibited a tendency to choose the pot on the right with its initial choice (binomial test, $p < 0.05$). There was no clear generic response pattern, since two subjects tended toward alternation and three subjects tended toward repetition of their two choices during a trial (table 7.1).

Not-Replace-Food Test

On this test, the elephant chose one of two baited pots, then received a food pellet on the second choice only if it chose the other pot. Subjects were tested to a criterion of eight alternations in ten trials. All subjects learned to alternate within 28 trials (mean number of trials to criterion = 19.6, including the three discarded trials; table 7.1). The response bias toward the pot on the right continued for four of the five subjects (table 7.1: binomial test; $p < 0.05$ in each case).

Inter-Rater Reliability

The Kappa coefficients of agreement for the three types of two-pot tests are presented in table 7.1. The lowest Kappa coefficient was 0.94, indicating a high level of inter-rater reliability.

Conclusions: Two-Pot Tests

Overall, the subjects exhibited a position preference to the right on their initial choices during a trial. This bias was weak during the no-food procedure, but strong for most of the subjects during both the replace-food and the no-replace-food procedures. Similar position preferences have been observed in other large herbivores (Hosoi, Rittenhouse et al. 1995; Hosoi, Swift et al. 1995). It is not clear whether the strong response biases represent hereditary predispositions of the elephants, perhaps related to their foraging styles, or result from the specific life experiences of these animals. Testing with other groups of elephants may clarify this issue.

Because of the response biases, the tendency toward spontaneous alternation was assessed using adjusted scores (Dember and Fowler 1958). There was a statistically significant rate of alternation under the no-food condition, in a manner typical of many other species (Richman et al. 1986). However, this tendency should be studied with forced choice, rather than free choice, procedures (Richman et al. 1986) to control for initial response biases, and with more subjects, before definitive conclusions can be drawn.

Table 7.2
Total number of trials conducted, mean choice accuracy for the last five trials, and inter-rater reliability (Cohen's Kappa coefficient) on the four-pot tests with the arc, semicircle, diamond, and square arrays.

		Subject					
Array	Measure	Cita	Ivory	Kubwa	Sophi	Tombi	Mean
Arc	Trials	11	12	10	12	12	11.4
	Accuracy	3.0	3.6	3.6	3.2	3.2	3.32
	Kappa	0.91	0.94	0.92	0.87	0.87	0.90
Semicircle	Trials	11	11	11	9	11	10.6
	Accuracy	3.8	3.8	3.8	3.6	3.8	3.76
	Kappa	1.00	1.00	1.00	0.96	1.00	0.99
Diamond	Trials	12	10	10	11	10	10.6
	Accuracy	3.0	3.4	3.6	3.2	3.4	3.32
	Kappa	0.94	0.93	0.97	1.00	0.93	0.95
Square	Trials	4	13	10	14	11	10.4
	Accuracy	3.25[a]	3.2	3.8	3.0	4.0	3.45
	Kappa	1.00	0.97	1.00	1.00	0.91	0.98

a. Cita completed only four trials under this procedure.

When food was introduced into the task in the replace-food condition, only two of the five subjects continued to alternate choices. This disruption of spontaneous alternation by the availability of food reward has been demonstrated previously with rats (Richman et al. 1986), although sometimes rats maintain a "win-shift" search pattern on the radial maze when all responses are rewarded equally (Olton and Schlosberg 1978). Ungulates exhibit a win-stay tendency under these conditions (Hosoi, Rittenhouse et al. 1995; Hosoi, Swift et al. 1995).

When the subjects were rewarded for alternating their choices, the "win-shift" strategy was acquired rapidly.

Four-Pot Procedures

Single-Pot Pre-Exposure

Each elephant was given trials on which it was allowed to open a single pot placed in one of four locations in the large stall (arc array, figure 7.1). The four locations were arranged along the arc of a 4.1-meter-radius circle centered on the mat which marked the elephant's starting location. Adjacent locations on the arc were separated by 2.3 meters. On a trial, the elephant was released by the handler and allowed to collect a single food pellet from the pot. The elephant was then called back to the start position. Elephants were tested 2–4 times with each of the four pot locations (a total of 8–16 trials, spread over 2 days).

Arc Array Pre-Training (Barn)

Before the tests in the arena, the elephants were tested with the arc array (figure 7.1) inside the barn. Each subject was tested once per day. For the first 20–25 trials, the reward in each pot was 1 food pellet. The reward was increased to 4 pellets for the next 10–15 trials.

Arc, Semicircle, Diamond, and Square Arrays (Arena)

The apparatus was moved to the outside arena, to determine whether the spacing of the food locations would influence choice accuracy. The spatial separation between food sources (Dale 1982; Douglas, Mitchell, and Del Valle 1974), or between food sources and nearby landmarks (Brown 1992) influences search strategies in other animals. The subjects were tested once per day, 4–5 days per week. The reward in each pot was four food pellets (29–30 grams). The elephants received 10–12 trials on the arc array (figure 7.1). The pots were 4.3 meters from the center of the start mat under the elephant's jaw, and 2.3 meters apart. The subjects next received approximately ten trials on each of three four-pot arrays. To visualize the patterns, imagine the elephant facing forward as being an orientation of 0° on a compass. The first arrangement (semicircle array, figure 7.1) placed the four pots in a semicircle around the elephant, with pots at 60° intervals. The pots were 4.3 meters from the center of the mat and 4.0 meters apart. In the second arrangement (diamond array, figure 7.1), pots were placed directly in front of and behind the subject, and to the subject's left and right. For this test, the elephant stood with the mat beneath its stomach, between the forelegs and the hind legs, between choices. The pots were 4.3 meters from the center of the mat for Tombi, Kubwa, and Ivory. Starting with Sophi's third trial, and for all of Cita's trials, the pots were placed 4.9 meters from the center mat. The larger circle was used for the two largest animals because they would occasionally reach toward the rear pot while they were standing at the center of the circle between choices. The final four-pot array was the square array (figure 7.1), in which the four pots were placed at 90° intervals around the subject, with pots 45° to the subject's left and right. The radius of the array was increased to 6.7 meters for all subjects, in preparation for the eight-pot tests.

The data for the tests with the arc, semicircle, diamond, and square arrays (figure 7.1) are presented in table 7.2.

Inter-Rater Reliability

The inter-rater reliability was high for all subjects. The lowest value of Cohen's Kappa for any subject on any test was 0.87, and the median was 0.965. The inter-rater reliability was lowest for the arc array, possibly because of the close proximity of the pots in this array.

Choice Accuracy

Choice accuracy for this phase of testing was measured by the number of different pots selected in four choices. Because of the strict choice criterion, there were a number of trials discarded during this phase of the experiment. Since an acquisition curve would mean little under these conditions, table 7.2 shows the total number of trials in the arena experienced by each subject and the mean choice accuracy over each subject's last five trials. Generally, the subjects were given 9–14 trials on each four-pot array. The median number of trials was 11. (Cita only received 4 trials on the square array.) The testing order was arc, then semicircle, then diamond, then square arrays. The mean choice accuracy for each subject on the last five (completed) trials in each condition is shown in table 7.2. A within-subjects ANOVA was carried out to compare choice accuracy across the four arrays. There was a clear effect of the Array factor: $F(3, 12) = 12.00$, $p < 0.01$. Orthogonal contrasts ($3X_{\text{semi}} - X_{\text{arc}} - X_{\text{diamond}} - X_{\text{square}}$: $F(1, 12) = 11.60$, $p < 0.01$; $X_{\text{diamond}} + X_{\text{square}} - 2X_{\text{arc}}$: $F(1, 12) = 0.28$, $p > 0.05$; $X_{\text{diamond}} - X_{\text{square}}$: $F(1, 12) = 0.83$, $p > 0.05$) indicated that choice accuracy was higher with the semicircular array than with the other three arrays, and performance was equivalent on those three arrays. The subjects' mean choice accuracy was above chance (random choice: 2.734 pots) for each of the arrays: arc array, (3.32), $t(4) = 4.88$; semicircle array, (3.76), $t(4) = 25.65$; diamond array (3.32), $t(4) = 5.75$; square array (3.45), $t(4) = 3.45$ ($p < 0.05$ in each case).

Response Biases and Patterns

Response biases were determined for each array by the distribution of "first choices" during all trials on that array. The distribution of "first choices" on each array was non-random for some subjects on each array. On the arc array, all of the elephants except Cita exhibited a side preference (binomial test, $p < 0.05$): Tombi was biased to turn left (83 percent of all trials: pots 3 and 4) whereas Ivory (83 percent), Kubwa (90 percent), and Sophi (83 percent) were biased toward turning right (pots 1 and 2). On the semicircular array, Tombi again had a "left-turn" bias (100 percent) and Ivory had a right-turn bias (100 percent; binomial test, $p < 0.05$). Kubwa (73 percent) had a non-significant tendency to turn left; Sophi (78 percent) had a non-significant tendency to turn right. With the diamond array, all five subjects showed significant response biases (binomial test, $p < 0.05$). Cita (92 percent), Ivory (100 percent), and Sophi (100 percent) tended to choose pots 1 and 2, whereas Kubwa chose pots 2 and 3 (100 percent) and Tombi chose pot 3 (100 percent). No subject ever chose pot 4 (behind the subject) with its first choice (0/53 trials). Finally, on the square array all subjects tended to choose the two pots in front of them at the start of the test (90.4 percent: pots 2 and 3). Individually, Ivory (85 percent), Sophi (100 percent) and Tombi (91 percent) exhibited significant "forward" biases. Kubwa exhibited a non-significant forward bias (80 percent). Cita (100 percent forward choices) completed only 4 trials under this condition.

Conclusions: Four-Pot Tests

The elephants had above-chance choice accuracies on all four arrays, although performance was best on the semicircular array. Perhaps this array presented the optimal task because the pots were spaced far apart and in front of the subject. Unlike the diamond and square arrays, the subjects were not required to turn around—contrary to their persistent, strong response biases—to obtain food.

Eight-Pot Procedures

The subjects were tested with an eight-pot array (figure 7.1), as an analogue of Olton and Samuelson's (1976) eight-arm radial maze apparatus. The pots were placed at 45° intervals around the perimeter of a 6.7-meter-radius circle, centered on the mat. Before each trial, each of the eight pots was baited with one apple. To begin a trial, the subject was placed in the center of the circle of pots (with its torso over the mat), facing pot 2. It was released by a handler, allowed to choose one pot, then was recalled and repositioned over the mat, facing pot 6 (turned 180°) between choices. The observer then walked around the circle of pots, touching every pot, and replacing the lid on the pot that had been chosen. Any mucus left on the pot lid was smeared on nearby pots. A second handler then took control of the elephant, turned it to face pot 2, and released it for another choice. The procedure continued, with the two handlers alternating, until the subject had made eight choices.

Inter-Rater Reliability

The inter-rater reliability was calculated for all eight-pot trials completed by each subject. Cohen's Kappa was at least 0.97 for each subject, indicating very high inter-rater reliability.

Choice Accuracy

Choice accuracy was measured by the number of different pots chosen during the subject's eight choices on each trial (table 7.3). Random selection under this procedure would produce an expected score of 5.25.

Data are reported for five-trial blocks from the first 25 completed trials for each subject (table 7.3). The numbers in parentheses indicate the number of incomplete (and therefore discarded) trials within each block. In addi-

Table 7.3

Choice accuracy on the eight-pot array: mean number of different pots chosen in eight choices. The number of trials discarded in obtaining each block of five trials is shown in parentheses.

Trials	Cita	Ivory	Kubwa	Sophi	Tombi	Mean
1–5	5.8(1)	7.2(4)	6.6(3)	6.2(1)	6.8(0)	6.52[a] (1.8)
6–10	7.0(1)	7.8(1)	6.8(2)	6.8(0)	6.8(1)	7.04[a] (1.0)
11–15	7.0(0)	7.6(1)	7.4(0)	8.0(0)	7.2(0)	7.44[a] (0.2)
16–20	7.4(0)	7.4(1)	7.6(2)	7.8(1)	7.0(1)	7.44[a] (1.0)
21–25	7.0(0)	7.2(1)	7.4(1)	7.8(0)	7.6(1)	7.40[a] (0.6)

a. Group mean choice accuracy is significantly above chance (random choice of pots), $p < 0.01$.

tion to the 23 incomplete trials, there were five trials on which a subject was faced "backwards," toward pot 6, to start the trial. Data from these five trials are not included. The group mean choice accuracy was significantly above that expected from random choice (5.25) for all blocks of five trials (smallest t value: for trials 1–5, $t(4) = 5.26$, $p < 0.01$). There was a significant improvement in choice accuracy across blocks of trials, $F(4, 16) = 5.80$, $p < 0.01$.

Response Biases and Patterns

The subjects exhibited several consistent response biases during the eight-pot test (table 7.4). All subjects tended to choose the pots in front of them (pots 8, 1–4, figure 7.1) when they were released, only selecting the pots behind them (pots 5–7, figure 7.1) toward the end of a trial. This tendency was assessed with three measures: The percentage of trials with the initial choice made to one of the front five pots; the percentage of the first five choices made to these five pots; and the percentage of errors (repetitions) made to these pots. For a subject choosing pots randomly, the expected value for each of these percentages would be 62.5 percent. The subjects' tendency to choose front pots exceeded chance by each of these measures. The mean percentage of first choices to the front pots was 98 percent; the mean percentage of the first five choices to the front pots was 90 percent; the mean percentage of errors to the front pots was 90 percent (Smallest t value: $t(4) = 11.5$, $p < 0.01$).

The response sequences exhibited by the subjects were evaluated in two ways: by the mean transition size and by the frequency of stereotyped

Table 7.4
Response biases on the eight-pot test: percentage of initial choices, the first five choices, and errors made to the front five pots; mean transition size and percentage of trials with a response pattern involving four or more consecutive choices.

Measure	Cita	Ivory	Kubwa	Sophi	Tombi	Mean
First choice (%)	100	96	96	100	96	98
Five choices (%)	87	90	91	94	90	90
Errors (%)	93	93	95	88	82	90
Transition size	2.07	1.83	2.21	1.81	2.11	2.01
Pattern (%)	56	36	8	44	20	33

choice sequences. The mean transition size was the average distance between the pots selected on consecutive choices, with the distance between adjacent pots being designated as one unit. The minimum transition size was 0 (returning immediately to the pot just selected); the maximum transition size was 4 (choosing the pot in the circle opposite to the pot just selected). A subject choosing pots randomly would be expected to have a mean transition size of 2.00, because each of the eight possible transition sizes (0, ±1, ±2, ±3, 4) would occur equally often. The mean transition size of the five subjects was 2.01, which did not differ from chance, $t(4) = 0.08$, $p > 0.05$. However, the distribution of transition sizes was not random. With random choice, each of the eight transition sizes would have occurred equally often, on 12.5 percent of the transitions. Overall, transition sizes of 4, 3, 2, 1, 0, −1, −2, and −3 occurred on 11.7 percent, 12.2 percent, 10.6 percent, 29.7 percent, 1.6 percent, 13.0 percent, 10.2 percent, and 11.0 percent of the transitions, respectively. In other words, subjects rarely returned to the same pot (transition size = 0), whereas choosing the "next pot to the left" was common (transition size = 1). The other six possible transition sizes occurred with near-chance frequencies.

To determine whether response algorithms might play a role in determining choice accuracy (Olton and Samuelson 1976), the frequencies of four possible response algorithms were measured: "adjacent" (e.g., 12345678) "alternate" (e.g., 24681357), "every third" (e.g., 14725836), and "opposite" (e.g., 15263748). In 125 trials, there was not a single example of a sequence of seven or eight choices made consistent with one of these algorithms. The criterion for a response pattern was a minimum of four consecutive choices during a trial matching the pattern (e.g., 1234, 2468, 1472, 1526). Adjacent, alternate, every-third and opposite patterns occurred on 26.7 percent, 0.8 percent, 0 percent, and 8.0 percent of all trials, respectively (table 7.4; on two trials, both adjacent and opposite patterns occurred).

The influence of response patterns on choice accuracy was assessed by comparing the mean choice accuracy on all trials with response patterns to that on all trials without such patterns. Although the mean choice accuracy on trials with a response pattern was higher than the mean choice accuracy on other trials, 7.33 vs. 7.07, the difference was not statistically significant, $t(4) = 1.29$, $p > 0.05$.

Table 7.5
Mean choice accuracy on the 8-pot test for the last five trials before, and the first five trials after a 6–8 month interruption of testing. In 1992 there were 4-pot and 8-pot tests. The date for the last test of each type is shown in the table.

	Last 1992 4-pot test	Last 1992 8-pot test	Choice accuracy	First 1993 8-pot test	Choice accuracy
Cita	Dec 12	Dec 9	7.2	June 28	7.8
Ivory	Dec 12	Dec 9	7.2	June 28	7.0
Kubwa	Nov 19	Oct 23	7.6	June 28	7.2
Sophi	Dec 12	Dec 9	7.4	June 28	7.8
Tombi	Nov 19	Oct 23	7.6	June 28	7.0
Mean	—	—	7.40	—	7.36

Conclusions: Eight-Pot Tests

The subjects chose pots accurately from the beginning of this phase of the study, with choice accuracy being above chance even for the first block of five trials. The elephants' choice accuracies were similar to those of other species tested on similar tasks (Olton and Samuelson 1976).

The subjects had a strong tendency to select the five pots in front of them at the moment they were released for a choice. This is not surprising, given that these pots were visible at the time of release and that they could be reached more quickly and (presumably) with less energy expenditure than that required to select the three pots behind the subject. However, the strong tendency to choose the "front-five" pots first implies an asymmetry in the sequence of choices. This asymmetry would reduce the likelihood of long sequences of patterned responses. For example, any sequence of six or more adjacent-pot choices (e.g., 123456) would require choices of some of the pots behind the subject at release (pots 5–7, figure 7.1). This "forward bias" may be why subjects did not show higher levels of response stereotypy. Although the elephants exhibited higher-than-chance proportions of adjacent-pot choice sequences, most of these sequences were only four choices long, as would be expected from a bias toward selecting the pots in front of the animal. The choice patterns which did occur were probably not simple response chains, since the subjects were turned 180° at the center of the circle of pots between choices. Similar adjacent-site choice patterns have been observed in other species (gorillas: MacDonald 1994;

rats: Dale and Innis 1986, Roberts and Dale 1981; pigeons: Spetch and Edwards 1986; pigs: Mendl et al. 1997; Siamese fighting fish: Roitblat, Tham, and Gollub 1982).

Smell-Control Procedures

After the standard eight-pot tests, each subject was given three types of smell-control test: one-choice smell-control (SM1) tests, four-choice smell-control (SM4) tests, and eight-choice smell-control (SM8) tests. Tombi and Kubwa received the eight-choice and the one-choice tests before the four-choice tests. The other three subjects were given the four-choice tests first.

One-Choice Smell-Control Test

Each subject received four SM1 tests inside the large stall in the barn (one test/day). The four pots were arranged in the arc array, with an apple in one pot. (The apple was in a different pot on each of the four trials.) The subject was released at the mat and allowed to select one pot. The elephant was then recalled to the mat, facing forward. The subjects found food on only 3 out of 20 trials (15 percent). This was not significantly different from chance accuracy (25 percent; $t(4) = 1.0$, $p > 0.05$).

Four-Choice Smell-Control Test

All subjects were tested on the arc array in the barn. Four food pellets were placed in each pot at the start of the test. Each subject was given seven standard tests, as described above, interspersed with seven smell-control tests. Before smell-control tests, a monkey-chow-and-water paste was smeared on the lid of each pot, and on the lids of three other replacement pots (in pans) kept in an adjacent room. During the trial, each pot (and pan) that the subject chose was replaced with a new pot (and pan). The observer touched all four pots between choices. Thus, the subject was always choosing among four pots that had not been touched previously, and the lid of each pot was covered with monkey-chow paste. Since Cita only completed five "standard" four-pot tests during this phase of the experiment, the choice scores were compared for each subject's first five standard tests and its first five smell-control tests. The group mean scores of 3.56 on the standard tests and 3.68 on the smell-control tests were not significantly different: $t(4) = 1.18$, $p > 0.05$.

Eight-Choice Smell-Control Test

Each subject except Cita was given six smell-control trials with the eight-pot array in the outside arena. These followed immediately after many standard eight-pot trials for Tombi and Kubwa, and after three standard eight-pot tests for Sophi and Ivory. Before each trial, each of the eight pots was baited with an apple. An "apple sauce" made from the same batch of apples was wiped on the lid of each pot, and on the lids of seven replacement pots (in pans) kept in the barn next to the arena. Between choices, the observer touched all eight pots in the array, replacing the pot and pan that the elephant had just chosen. Thus the elephant was always choosing among eight pots it had not touched, and the lid of every pot was coated with apple sauce. Only those pots in previously unchosen locations contained an apple. Since Ivory only completed three trials under the smell-control procedure, data are presented for each subject's first three smell-control trials, and its last three standard eight-pot trials. The mean scores of 7.67 on the standard trials and 7.58 on the smell-control trials were not significantly different, $t(3) = 1.0$, $p > 0.05$.

Conclusions: Smell-Control Tests

The subjects' mean choice accuracy on the four-choice and eight-choice smell-control tests was above-chance and comparable to performance on the standard four-pot and eight-pot tests. On these smell-control trials, the possibility that the elephants were leaving scent cues on the pots was removed and any scent from the apples (or food pellets) in the closed pots was probably masked by the apple sauce (or food-pellet paste) on the lids of the pots. There is no evidence that these manipulations disrupted choice accuracy. However, we are only beginning to understand the complexities of elephant olfaction (Rasmussen and Krishnamurthy 2000). Thus, we must remain open to the possibility that the food paste or apple sauce on the lids did not smell the same as the reward in the pots and, consequently, may not have adequately masked the scent of the reward. For this reason, the fact that that the subjects chose with chance accuracy on the one-choice test is important. The subjects had the opportunity to detect an apple in one of four pots without any masking cues present, yet did not do so. In combination, the results indicate that olfactory cues were not important during the three tests described above. They are consistent with the results of experiments with other species showing that olfactory cues do not determine performance on spatial memory tests (Dale and Bedard 1984; Suzuki, Augerinos, and Black 1980; Zoladek and Roberts 1979).

Overall, this series of studies extends the demonstration of short-term spatial memory abilities to the African elephant, and suggests that neither response algorithms nor olfactory cues play a major role in determining choice accuracy. These conclusions are similar to those drawn from a variety of other species (e.g., Olton and Samuelson 1976). The data obtained with elephants are similar to those obtained with other large herbivores, especially on the two-pot tests (cattle, Hosoi, Rittenhouse et al. 1995; goats and sheep, Hosoi, Swift et al. 1995).

Long-Term Retention of Test Procedure

Testing was interrupted for 6–7 months (over the winter) then all five animals were re-tested on an eight-pot procedure identical to the standard eight-pot procedures described above. After the interruption, subjects were tested about twice per week. The purpose of the experiment was to determine whether task performance would be retained over the interim period (Dale, Shyan, and Hagan 1994b). Table 7.5 shows choice accuracy on the last five eight-pot tests before the interruption, and for the first 5 tests after the interruption. Since not all of the subjects were treated identically before the interruption, table 7.5 shows the dates of the last four-pot and the last eight-pot test for each animal. The last five tests in 1992 were standard eight-pot tests for Cita, and smell-control tests (SM8) for Kubwa, Sophi, and Tombi. For Ivory, the final eight-pot tests during 1992 included three smell-control (SM8) tests and two standard eight-pot tests. Data presented above suggest that choice accuracy did not differ on standard eight-pot tests and SM8 tests, so that the differences between test procedures can be ignored. Mean choice accuracy before the break (7.40) was not significantly different from that after the break (7.36), $t(4) = 0.17$, $p > 0.05$.

After 5–6 standard eight-pot tests, each subject was exposed to 5–7 trials with a modified (more elaborate) smell-control test. On these "SM8Drag" trials, two heavy chains attached to a 10-foot (3 meters) board were dragged around the center of the circle of pots after every choice. These chains swept the surface of the dirt arena, so that all footprints on a 2.6-meter-wide track of ground inside the circle of pots were eliminated. The chain dragging also distributed any "smell-contaminated dirt" around the circle.

In addition, every pot the elephant chose was replaced with a fresh, empty pot (and pan). The lids of all pots involved in the trial were covered with an apple sauce made that day from the test apples. The apple sauce was "chunky," so that the lid of each pot was smeared with pieces of apple, apple skin, apple paste, and apple juice. These elements should have produced a variety of odors to mask the smell of an intact apple inside the closed steel container. Based on a sample of 4–7 trials per subject in each condition, these precautions produced a small, non-significant increase in the mean trial duration: From 13.1 minutes (standard trials) to 14.5 minutes (SM8Drag trials), $t(4) = 2.48$, $p > 0.05$. The increase in trial duration was not longer because two observers participated in these trials: One to drag the chains and one to replace the pots.

The mean choice accuracy of the 5 elephants dropped slightly during the smell-control trials, $t(4) = 2.99$, $p < 0.05$ (7.44 for 5–6 standard trials/subject; 7.02 for 5–7 SM8Drag trials/subject). However, the mean choice accuracy on the smell-control trials remained far above chance, $t(4) = 9.51$, $p < 0.05$.

Conclusions: Retention Tests

The elephants exhibited high choice accuracy after the 6–7-month interruption, starting with the very first day of testing. This indicates that the reference-memory components of the task are well retained. This is consistent with anecdotal evidence concerning the elephant's excellent long-term memory (Shoshani 2000).

Proactive Interference with Multiple Tests

The elephants were tested on a variant of the eight-pot test—a serial-position test procedure—in 1994 (not reported here), then returned to the standard eight-pot test in 1995 (Dale, Peterson, and Shyan 1995). The elephants were tested on two eight-pot arrays, the standard array, and an array rotated 22.5° clockwise, so that four pots were in front of the elephant at the start of each choice, and four pots were behind it (rotated array).

Initially, Kubwa and Tombi were each tested on 5–6 standard eight-pot trials (mean choice accuracy = 7.36), then on 5–6 smell-control trials (SM8Drag tests: mean choice accuracy = 7.36). Since both did well from the beginning of testing, the other three elephants were started directly on the three-trials-per-session procedure when Kubwa and Tombi were switched to that procedure. Kubwa and Tombi received 15 and 12 sessions, respectively; the other three elephants each received 13 sessions. Cita, Ivory, Kubwa, Sophi, and Tombi completed 11, 11, 13, 11, and 12 trials successfully. Five trials were discarded because of "double touches," two were discarded because of handler error (calling an elephant back before it made a choice), and one trial was discarded because of observer error (stopping a trial too early).

All five elephants were placed on the one-trial-per-session procedure for 4–6 sessions with the standard eight-pot array (figure 7.1), then returned to the three-trials-per-session procedure. Cita and Ivory received 7 and 8 sessions on this procedure, respectively. The other three subjects each received 6 sessions. Only one session was discarded, for Cita, because of a double touch.

Except for the 22.5° rotation, the two eight-pot arrays were identical. The data from both arrays were analyzed in a single two-factor, within-subject ANOVA, using the mean choice scores on the first (rotated) array and on the second (standard) array. The analysis was a 2 (arrays) × 3 (trials within a session) design (table 7.6). There was a significant effect of trials, $F(2,8) = 6.22$, $p < 0.05$. Neither the array factor, $F(1,4) = 7.31$, $p > 0.05$, nor the trials × array interaction, $F(2,8) = 0.92$, $p > 0.05$, produced significant effects. *Post hoc* orthogonal contrasts indicated that choice accuracy on trial 1 was higher than the average choice accuracy on trials 2 and 3, $F(1,8) = 11.59$, $p < 0.05$, but that there was no difference in choice accu-

Table 7.6

Choice accuracy when the elephants were given three trials within a session: number of different pots selected in eight choices during a trial. Data are presented for both the standard array (figure 7.1) and the rotated array.

Array	Trial	Cita	Ivory	Kubwa	Sophi	Tombi	Mean
Rotated	1	6.36	6.18	6.18	6.00	7.09	6.36
	2	6.36	6.27	6.18	5.91	5.91	6.13
	3	6.18	5.73	5.73	5.82	5.73	5.84
Standard	1	6.67	7.33	6.83	7.00	6.83	6.93
	2	6.17	6.33	6.50	7.17	6.17	6.47
	3	6.33	6.50	6.00	7.17	6.50	6.50

racy between trials 2 and 3, $F(1,8) = 0.83$, $p > 0.05$. In other words, the drop in choice accuracy occurred between trials 1 and 2.

Conclusions: Proactive Interference Tests

Despite the major differences in species, apparatus, and procedure, the data indicated a pattern of proactive interference similar to that obtained with rats on a radial maze (Roberts and Dale 1981).

General Conclusions

Captive African elephants exhibited spontaneous alternation and high choice accuracy when selectively rewarded for a "win-shift" strategy on two-pot, four-pot, and eight-pot tests. They did so despite strong response biases and tests that lasted up to 15 minutes. This is impressive for animals that were tested without food deprivation and rewarded with treats. The memory for visited locations was disrupted by giving three tests in rapid succession, but the retention of reference-memory components of the task was long-lasting.

Several types of smell-control tests indicated that the disturbance of olfactory cues had, at most, a minor effect on choice accuracy. The elephants apparently did not depend on food-smell cues or self-generated odor trails to find the food.

Theoretical Model

John Staddon recently defined theoretical behaviorism as "the study of the mechanisms of behavior, where *mechanism* is whatever works to account for behavior" (2001b, p. 143). So far, our research group has demonstrated that elephants search for food systematically, and that the search is guided, in part, by spatial memory. We have presented the "behaviorism" component of John Staddon's theoretical behaviorism, but what about the theoretical part?

I will outline a preliminary, but promising, two-dimensional model derived from a perceptual metaphor: the "Beam" model. (For other uses of perceptual metaphors, see Staddon 1983.) Imagine a beam of light projected by a floodlight (figure 7.2). The bulb itself represents a location in

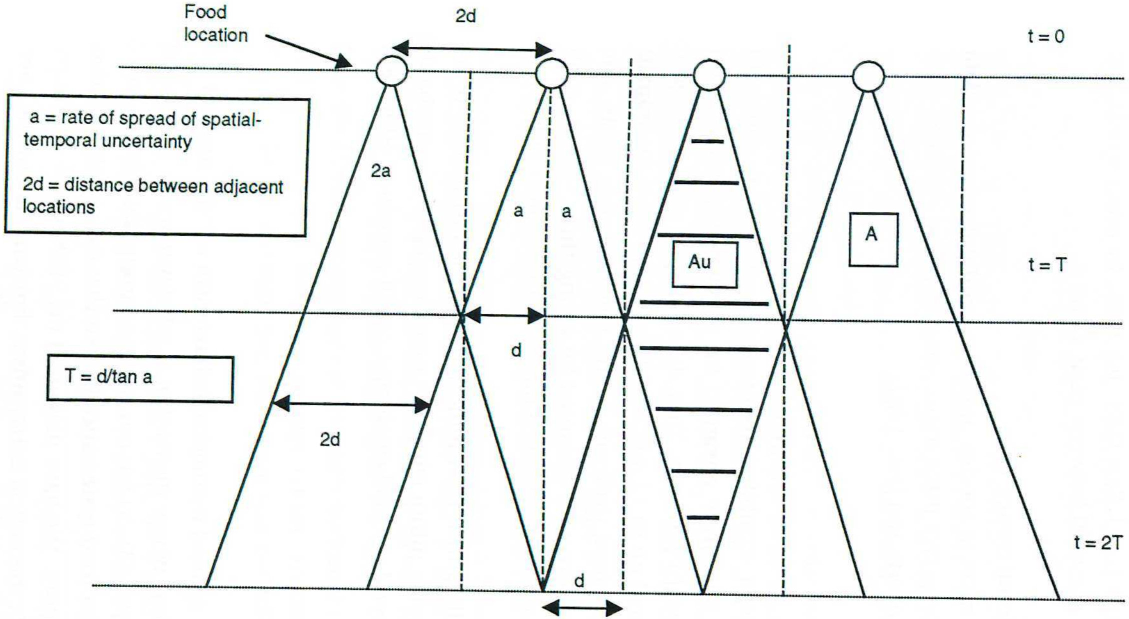

Figure 7.2

The "Beam" model: The uncertainty of the memory for each location increases linearly with time. Assuming equal spacing of the food locations, the memory for each location has a valence, V_i. $V_i = 1$ until time T (i.e., no forgetting/confusion of separate locations). After time T, the memory trace decays in an S-shaped (though almost linear) curve. After time $2T$, the valence decreases as a power function of time. There are two parameters in the model: $2d$ = the distance between adjacent locations and a = an angle representing the rate of increase in spatial-temporal uncertainty. There is a discrimination threshold (DV), above which location valences are distinguishable from 0. $DV = V_{max}/k$, where V_{max} is the maximum possible valence for any of the locations involved and k is a sensitivity constant.

space. The light beam spreads at a constant rate, with the width of the beam representing the subject's degree of uncertainty of the bulb's spatial location. Figure 7.2 depicts four locations and their associated beams of light. The beam from each location expands over time. At first the four beams do not overlap, and each location can be discriminated from its neighbors with complete accuracy. After a time period T, the light beams begin to overlap and the locations can no longer be distinguished perfectly. After a time period $2T$, each light beam is completely overlapped by the beams from adjacent locations.

The valence (V) of the memory trace for each location at time t is determined by the area of the unique or non-overlapping portion of a beam (that is, the initial section of the beam: Au) divided by the total area of the beam at that time (A): $V = Au/A$. Unvisited locations will have valences set at zero. The valence is reset to a value of C when the location is visited—and remains constant for specific period of time (T). T is determined by the rate at which beam spreads ($2a$ = angle of dispersion of the beam) and on the distance, $2d$, between that location and each of its neighbors. In fact, $T = d/\tan(a)$. I will make four simplifying assumptions in my discussion of this model:

1. A location's valence is reset to $C = 1$ whenever it is visited.
2. The valence of each visited location gradually declines from 1 to (almost) 0.
3. All adjacent locations are the same distance ($2d$) apart.
4. The beam spreads at a constant rate ($2a$ = the angle subtended by the beam, in radians).

With these assumptions, the valence of a location at time t after it has been visited is given by the following equations (figure 7.2): For $0 < t < T$,

$$Vi = Au/A = 1,$$

where Au = non-overlapping (unique) area of beam, A = total area of beam, and $T = d/\tan(a)$. For $T < t < 2T$,

$$Vi = 4T/t - 2T^2/t^2 - 1.$$

For $t > 2T$,

$$Vi = 2T^2/t^2.$$

Although the perceptual metaphor above represents memory in a straightforward manner, it does not translate into a simple mathematical function. The memory trace function has three components: An initial constant value, then a brief S-shaped section, then a power function. The validity of these equations was confirmed graphically—they predicted several values of V $(= Au/A)$ computed from scaled drawings of the overlapping beams.

Several features of the model deserve comment. One is that spatial and temporal dimensions are integrated into a single memory variable (V). At first glance, such an integrated memory trace may seem implausible. However, there is evidence that animals make this type of spatial-temporal integration (Cheng, Spetch, and Miceli 1996; Clayton, Yu, and Dickinson 2003). A second feature is that, at least after time $2T$, valence is described by a power function with two free parameters (a, d). This prediction is consistent with suggestions that numerous and varied sets of memory data are best fitted by a power function (Rubin, Hinton, and Wenzel 1999; Rubin and Wenzel 1996; Sikstrom 2002).

The model also claims that the valence of a location does not begin to decrease until a fixed time T after that place has been visited. Although this feature of the model is driven by the underlying perceptual metaphor, it overcomes one of the major criticisms of previous power-function models—namely, that the function is undefined at time, $t = 0$ (Sikstrom 2002; Wickens 1998). In fact, Sikstrom (2002) has suggested an elaborate connectionist model that—under specific constraints—also generates a forgetting curve that is a power function defined at time 0. Both models suggest a "lag" between the occurrence of an event and the start of forgetting. That two such different approaches—a connectionist model and a perceptual metaphor—result in similar forgetting functions is intriguing. These apparently disparate perspectives may be converging on the same (and perhaps previously ignored) characteristic of memory. It is also quite surprising that the model predicts a sigmoidal memory trace between times T and $2T$. However, empirically speaking, the S-shaped segment of the curve seems almost linear and is short enough that distinguishing it from a power function would be difficult (especially were one not looking for the alternative).

Having discussed the nature of the memory trace for an individual event, I should describe how performance on the spatial memory task is determined. Suppose that the subject compares the valences of all of the food locations before choosing one. The model assumes that the discrimination threshold is a constant proportion of the largest valence of any location relevant to the task. This would seem to be a simple application of Weber's Law to discrimination among memory traces, although the relationship between Weber's Law and timing may be more complex than recently believed (Dragoi, Staddon, Palmer, and Buhusi 2003; Fetterman and Killeen 1992; Grondin 2001).

To predict choice accuracy on the eight-pot spatial memory task, I assumed constant inter-choice intervals (as is often observed). The response/decision rule was that the subject choose randomly among locations with sub-threshold valences, while avoiding the other locations. (Note, however, that one could easily replace the random-choice rule with a specific set of response biases.)

Given these assumptions, the model predicts mean choice-accuracy scores of 6.72 (out of 8) with a valence discrimination threshold of 0.10 (Weber fraction = 1/10) and 7.75 with the valence discrimination threshold set at 0.05 (Weber fraction = 1/20). At the very least, the Beam model predicts choice accuracy in the empirically observed range and has several theoretically desirable characteristics.

In summary, the Beam model provides an alternative perspective from which to describe the behavior of elephants on a commonly used spatial memory task. Professor Staddon's facility and creativity with such quantitative modeling constantly refreshes my respect for him—rejuvenation, if you will.

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