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# Bonobo (*Pan paniscus*) Spatial Memory and Communication in a 20-hectare Forest

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*We used an artificial language as a tool for the study of spatial memory organization in a young* Pan paniscus. *In the first experiment, we showed the bonobo a road sign just outside its indoor sleeping area. The sign indicated, by means of arbitrarily designated geometrical shapes (lexigrams), where food was hidden. Only 2 of the 15 locations were visible from the sign. Distances ranged up to 170 m from the sign. In 99 of 127 test trials the bonobo went directly to the designated location on its first move. In a second experiment, we presented the road sign at varied points in the woods rather than at the original fixed place. In these trials the goal was a preferred toy. The bonobo's human companions were never told the location of the goal and distances were up to 650 m. In all 12 trials the bonobo led its companions to the designated place via an efficient path. The bonobo appeared to be able to move, based on the information provided by a lexigram, from almost any arbitrary starting location in its 20-ha environment to any one of the numerous goal locations.*

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**KEY WORDS:** spatial cognition; primate; great ape; chimpanzee; *Pan paniscus*.

This study examines the following questions. How accurately can a young symbol-competent male *Pan paniscus* that has been taken into the woods every day by human companions remember the general layout of a large outdoor environment and the locations of various places where he has obtained food? How consistently and effectively can he utilize arbitrary road signs which signal the presence of food or other objects at locations

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that are not visible at the time of choice? Can he still perform effectively when the road signs and the goal locations are separated by hundreds of meters?

Previous studies, including those on ape language, have not examined how apes use arbitrary visual signs to discriminate the presence of goal objects at locations that are at great distances from the sign. Furthermore, we know of no previous study of nonhumans that has clearly shown that an animal can go from an arbitrary starting location in a forest to any one of a sizeable number of distant goals. The issue of how flexibly animals can recall and go to different goals from different starting locations is a basic one in studies of animal spatial learning (Benhamou *et al.*, 1990; Boesch and Boesch, 1984; Byrne, 2000; Collett, 1996; Gallistel, 1990, p. 154; Garber, 1989, 2000; Janson, 2000; C. Menzel, 1991; E. Menzel, 1973a; R. Menzel, *et al.*, 1996; Sigg and Stolba, 1981; Woodworth, 1958). For example, Muller *et al.* (1996, p. 669) listed "the ability to find a straight-line path between any pair of points in the environment, so that any point can serve as a starting location and any other point can serve as a goal" as one of 3 definitive types of evidence for cognitive maps in animals, the other two types of evidence for generalized mapping skills being "the capacity to find shortcuts when a path is suddenly opened that is more efficient than the current path" and "the ability to find an optimal detour when a more efficient route is suddenly blocked" (Muller *et al.*, 1996, p. 670).

Here, we shall use the communication system that a bonobo had learned from people principally as a tool to examine his spatial memory. We treat questions regarding language or communication per se secondarily. That is to say, we shall focus on the bonobo as a receiver rather than as a sender of information. Elsewhere we have addressed questions regarding whether *Pan* spp. can intentionally use lexigrams (C. Menzel, 1999; Savage-Rumbaugh *et al.*, 1986) or can produce other signs (Savage-Rumbaugh *et al.*, 1996) to indicate where they are going, as well as whether they can read signs produced by others, and we will not get into these questions here.

In the first experiment, we examined whether the bonobo could travel from his home base to any one of 15 distant goal locations on the basis of the information contained in a lexigram road sign. In the second experiment, we studied his ability to go to different goals from different starting locations. In detail, we examined how effectively the bonobo could perform if he started out from a random point in familiar terrain and whether he could retain the information from a road sign and sustain his motivation and sense of goal direction long enough to travel to destinations that were hundreds of meters away and not visible throughout most of the journey. We presented the road sign (and the bonobo's starting point) at different locations in the woods rather than at a single location, and distances ranged up to 650 m.

## METHOD

### Subject

The subject was a juvenile male *Pan paniscus*, Kanzi, 4 years old at the start of the experiment. Savage-Rumbaugh *et al.* (1986, 1993) describe his rearing history and the manner in which he acquired facility in the use of lexigrams.

### Preliminary Experience

Prior to this study, we had not trained Kanzi formally in the use of lexigrams. He initially began to use lexigrams as an infant after watching experimenters try to teach lexigrams to his adoptive mother (Savage-Rumbaugh *et al.*, 1986, 1993). From 2.5 years of age (beginning 18 mo before this experiment) Kanzi had accompanied his human companions daily on excursions in the 20-ha forest and around the laboratory facilities (Savage-Rumbaugh *et al.*, 1986). During outings, Kanzi's human companions had used place names in spoken English, had pointed toward locations, and had touched lexigrams on a portable keyboard to announce travel destinations. Kanzi's companions had not merely placed lexigrams at a named place. Instead, they had pointed to the lexigrams, talked about them, accompanied their presentation with other relevant potential signs, such as photographs, of where they were going, and did so at any given point along the trail, wherever appropriate (Savage Rumbaugh *et al.*, 1993). Outings had not followed a predetermined route or timetable. If Kanzi indicated an interest in a new direction, the companions and Kanzi took it. The companions frequently pointed to and talked about place lexigrams without any travel ensuing. Thus, there had not been any fixed relationship between a caretaker touching a lexigram and the event of moving to that location. Despite the fact that the outings were not structured as formal training sessions, before the onset of this experiment, Kanzi began to select lexigrams corresponding to sites in the woods, and it appeared that he could lead a person to the site he had selected, even when the person had no knowledge of the location (Savage-Rumbaugh *et al.*, 1986).

### Apparatus for the First Experiment

About 3 m outside the door of the laboratory room in which Kanzi was housed at night, we drove a 1.5-m wooden stake into the ground. On the

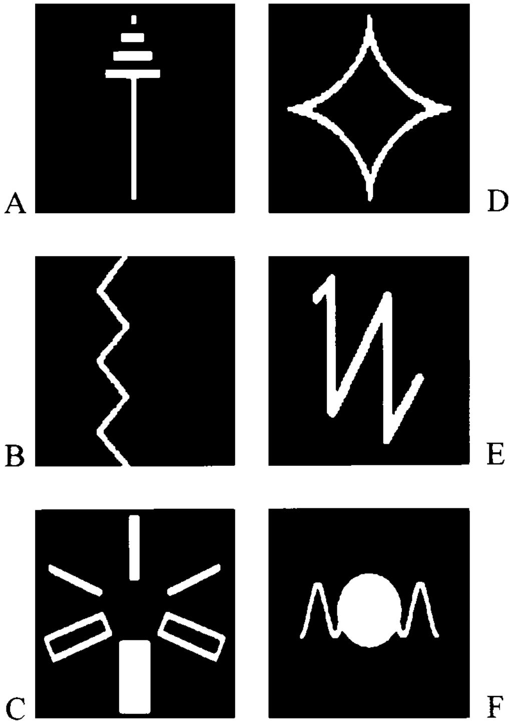

**Fig. 1.** Examples of lexigrams used on the road sign. a) dog pen, b) garden digging plot, c) staff office, d) trailer, e) colony room, f) food.

stake was a small board, onto which we hung lexigrams to serve as road signs (Fig. 1). Rumbaugh (1977) and Savage-Rumbaugh (1986) describe the principles by which lexigrams were originally designed. The lexigrams are obviously arbitrary when compared to the signs of distant food sources that wild bonobos might employ, and we assume that they would also be neutral or meaningless to an animal that lacked relevant experience (such as Kanzi had had) with them. Most of the test area was heavily forested and moderately hilly, and only 2 of the 15 sites that were used in the experiment for the introduction of food could be seen from where the sign was located. From 13 of the 15 food sites it was also impossible to see any other food site. At all times each of the 15 sites contained an identical insulated cooler, which served as a food container. The coolers themselves were never visible from where the sign was located.

## Test Procedure for the First Experiment

In the morning and again in the afternoon, for two trials per day, we placed Kanzi's rations for that portion of the day inside a food container at one of the 15 fixed sites. We used the more distant sites less often than closer ones, and they were not used on very cold or rainy days. Otherwise the sequence used for site selection was random. We hung 2 lexigrams on the wooden stake. One of them was FOOD, and the other lexigram corresponded to the site that contained food on that occasion, e.g. A-FRAME, SCRUBBY PINE NOOK, PLAY YARD.

Kanzi could initiate searching for food at any time by moving to the door, or by leading his human companion to the road sign, or by touching FOOD on the keyboard. The companion accompanied Kanzi to the road sign and allowed him to lead the way. In a typical trial, as soon as Kanzi saw the road sign he would run 10 m or more ahead of the person, seldom looking back, and the person had to hurry to keep up with him.

Kanzi could visit any number of sites during a trial. Once Kanzi found and opened the cooler that contained the food, the companion gave him a small amount of the food and then carried the remainder back to the lab for later consumption. The companion recorded each station that Kanzi visited. A visit was scored to a station if Kanzi touched the cooler. We conducted 127 trials over a 5-mo period.

Our aim was to assess what Kanzi had already learned about locations and about location lexigrams, and how well he could transfer his learning to new travel problems. Accordingly, the task was novel for Kanzi in several specific respects. First, before this experiment, we had never presented Kanzi with a randomly selected lexigram and then, in addition, required him to lead a person to the corresponding place. Second, we had never restricted his daily rations to a single location in the woods and required him to search for the single food source. When food was available in the woods in the past, a small amount had been present at each food site. Third, Kanzi had never encountered a lexigram hung on a post or a lexigram deliberately left in the environment as a sign or message that he had to interpret. Fourth, we had never required Kanzi to lead a person to any specific food site from a starting point near his home cage. We do not intend to imply by these statements, however, that Kanzi brought no relevant experience to the test situation.

## Analysis of First Experiment

We used Monte Carlo (randomization) tests to assess Kanzi's performance statistically, that is, to compare his performance to that expected by chance. Bullock and Stallybrass (1977, p. 400) define Monte Carlo methods as "the estimation of quantities (which are perhaps too difficult to calculate analytically) by construction of a probabilistic process which is then simulated using random numbers; the Laws of Large Numbers will guarantee that after a large number of runs of the simulation the estimated parameters of the model are unlikely to be far from the true values." The tests were both more conservative and more realistic than simply assuming the probability of correct response to be 1/15 and applying a Sign Test. Taken together, they should overcome the impossibilities of specifying exactly how many actual choice points one test situation contained and what the chance probabilities were of any given response. Three of the tests were as follows.

The first simulation consisted of one million Monte Carlo runs. On each run, for each of 127 simulated trials the Monte Carlo program picked one of the 15 experimental food locations using the same probability of responding to each location that Kanzi had on his first response. Having the Monte Carlo program's probability of responding to each location match Kanzi's probability controlled for response biases. Then we calculated the Euclidean distance between the place that the Monte Carlo program selected and the place at which the food had been located on the same trial and compared this distance with the corresponding distance of the first place to which Kanzi had moved on the same trial. If Kanzi's distance from the goal was shorter, he won on that trial. The question was whether Kanzi won significantly more trials than the Monte Carlo program.

The second simulation differed from the first in one main respect: we made the Monte Carlo program's probability of responding to each place match the total number of times that Kanzi had obtained food, that is, the frequency of reinforcement, at each location. The question was again whether Kanzi reliably won more trials than the Monte Carlo program.

In the third simulation, we compared Kanzi's performance against the chance-expected number of moves that he would have required to hit the goal if he had not used the roadsign as a cue. The Monte Carlo program picked one of the 15 places, using the same probability of responding to each location that Kanzi had on his first response. If the program failed to hit the goal on its first response, then it picked another place. If it missed the goal again, it picked another place, and so on, until it hit the goal. The Monte Carlo program picked locations without replacement. The question was how many of the 127 goals the program hit by its 1st, 2nd, . . . , nth response and how these frequencies compared with Kanzi's performance.

## Paths From Different Starting Points (Control Experiment)

In the main experiment, Kanzi always started out by the same fixed location, right by his home base. In a second experiment, we presented the road sign and Kanzi's starting point at varied points in the woods rather than at the original fixed place. The goal was not always food. Kanzi's human companions were never informed as to the location of the goal. Kanzi could never see the goal from the starting point, and straight-line distances ranged between 75 and 650 m.

We conducted Trial 1 of the control experiment when Kanzi was 2.8 years old and had only been travelling in the woods with caretakers for 4 mo. This trial preceded the main experiment by 1.2 yr; we include it only for the sake of completeness. We conducted Trials 2–12 over a 9.5-mo period, beginning when Kanzi was 4.7 years old. We conducted trials at irregular intervals, with no more than 1 trial per week.

While Kanzi was confined to his home cage and could not see what was occurring, an experimenter hid a goal object in the forest. Hiding occurred at least 1 hr and as much as 48 hr before the test was scheduled. The goal was food on Trial 1 and a preferred toy (plastic ball) on Trials 2 through 12. After the the goal was hidden, Kanzi was taken on an outing in the forest and given a cue as to where the goal was located. On Trial 1, a person who had never previously heard of the goal site and who did not know where it was located said to Kanzi in English "Take me to mushroom trail." On Trials 2 through 12, one person indicated "Ball" and the name of the goal site to Kanzi, both in spoken English and by touching these lexigrams on a portable keyboard. (On Trial 11, Kanzi was given a cue of the goal site twice.) The person who gave Kanzi the cue in the forest did not face or point in the direction of the goal when giving the cue. A second person—uninformed person—waited at a distance while Kanzi was given the cue. The uninformed person could not hear or see the cue and did not know where the goal was located. The person who gave Kanzi the cue then left the scene, and Kanzi could approach and interact with the uninformed person. When Kanzi joined the uninformed person, Kanzi typically vocalized, gestured down the trail, and headed out along the trail. The uninformed person allowed Kanzi to lead and recorded Kanzi's path of travel on a map of the forest.

## Analysis of Trials From Different Starting Points

Our analysis compared Kanzi's path of travel to the least-distance path, according to the following logic. The most generic measure of the distance between points A and B is the minimum number of idealized steps, all equal in length, that one would have to take to get from A to B. Similarly, the optimal travel path from A to B (in terms of least distance) would be a path that on any given step reduces the remaining distance to B by the length of that step. If space meets the assumptions of Euclidean geometry, i.e., the space is homogeneous, isotropic, and contains no barriers, then the optimal path will, by Euclid's own definition, be a straight line. But under any circumstance, if one were to plot a graph with "distance travelled thus far" on the X-axis and "distance from here to point B" on the Y-axis, all points from a perfectly efficient path would fall on a straight line, and the normalized linear regression slope of this line would be −1; equivalently, the ratio of total travel distance (D) to minimum possible distance (MinD) would be 1, and the Pearson product moment correlation between distance travelled thus far and distance from here to point B would be −1. Hence, two highly reasonable measures of the relative efficiency of any given path are the ratio D/MinD and r-squared.

Accordingly, for each of the 12 control trials, we digitized the map record of Kanzi's path of travel via a Genius Model HiSketch 1212 cadboard, and from the data points we calculated an r-square between Kanzi's travel distance so far and his straight-line distance now, from here to goal. Because the number of discrete data points used to characterize a travel path (N for each r-square) was to some extent arbitrary, we made 6 independent estimates of r-square on each map and report their mean values. For each of the 12 control trials, we also calculated the ratio D/MinD. Several-fold variations in N on the paths changed r-square and D/MinD only slightly. (Mathematically speaking, any straight-line segment of a path can, almost by definition, be fully characterized by two points.)

Our analyses assume no hills, swamps or barriers and completely ignore the trails shown on the maps. Thus, our analyses of Kanzi's efficiency of travel are highly conservative.

## RESULTS

### First Experiment

In 99 of 127 test trials, the first experimental location that Kanzi went to was the one that had been designated by the lexigram on the road sign (Table I).

In all 3 Monte Carlo analyses, Kanzi's performance greatly exceeded that expected by chance. The overall results of the first Monte Carlo analysis were that Kanzi won on an average of 96.8 trials, the Monte Carlo program

**Table I.** Number of times that Kanzi went first to each location, according to the number of times that each location was baited

| Location number | Distance (m) | Baiting frequency | Kanzi's frequency | Correct | % Correct |
|---|---|---|---|---|---|
| RS | — | — | — | — | — |
| 1[a] | 21 | 6 | 7 | 6 | 100 |
| 2[a] | 24 | 25 | 22 | 22 | 88 |
| 3 | 50 | 10 | 20 | 8 | 80 |
| 4[a] | 12 | 11 | 10 | 10 | 91 |
| 5[b] | 23 | 4 | 4 | 3 | 75 |
| 6[b] | 48 | 10 | 5 | 5 | 50 |
| 7 | 30 | 21 | 28 | 18 | 86 |
| 8 | 87 | 9 | 4 | 3 | 33 |
| 9 | 104 | 4 | 2 | 2 | 50 |
| 10 | 57 | 6 | 5 | 5 | 83 |
| 11 | 57 | 9 | 9 | 8 | 89 |
| 12 | 133 | 2 | 1 | 1 | 50 |
| 13[a] | 18 | 3 | 2 | 2 | 67 |
| 14 | 170 | 2 | 1 | 1 | 50 |
| 15 | 54 | 5 | 7 | 5 | 100 |
| Sum | | 127 | 127 | 99 | |

*Note.* Correct = number of correct choices (the location was baited and Kanzi went there first); RS = roadsign.
[a] Inside the laboratory building.
[b] Visible from roadsign.

won on an average of 14.1 trials, and the remainder (from 127) were ties. We computed a Sign test at the end of each run through the 127 trials. All $10^6$ Sign tests exceeded the value required for significance at $p < 0.001$; the worst of all $z$ scores was 5.83. The overall results of the second Monte Carlo analysis were almost identical to those of the first analysis. The results of the third Monte Carlo analysis were that the average number of goals that Kanzi hit on his first response (99 of 127) was about the same as the average number of goals that the Monte Carlo program hit by its 10th response (95 of 127).

When Kanzi did not hit the goal on his first move, his second move brought him closer to the goal on 74% of occasions. In 127 trials Kanzi made only one repetitive error: going back to the same location twice. Altogether, Kanzi went first to an incorrect location on 28 trials. On 24 of them, Kanzi's error was to go first to one of the three closest sites (3, 7, and 15) that was outside the building. Sites 3 and 7 were attractive to Kanzi, in part, for social reasons. From site 3, Kanzi could see people through windows in the laboratory building, and from site 7, he could see other apes in cages.

To examine whether Kanzi showed a change in the accuracy of his performance across trials, we examined the data by 20-trial blocks. On all 6 blocks, Kanzi went to the correct place on his first move significantly more frequently than would be expected by chance; the worst Sign test *z* score of the 6 was 5.6, $p < 0.0001$. Kanzi was less accurate on trials 1–20 than on trials 101–120 (70 vs 95% correct), but his first 5 trials were errorless, and overall the product-moment correlation between the ordinal number of the trial and correct vs incorrect was $r = .12$ ($N = 127$; n.s.).

## Paths From Different Starting Points (Control Experiment)

On 3 of the 12 control trials, Kanzi climbed on the uninformed person within 10 m of the start location (Trials 3, 8, and 9). When Kanzi rode, he guided the uninformed person by extending his arm, by leaning to one side, and by moving the person's face with his hand. Before the uninformed person had come close enough to see the goal object, Kanzi jumped down and ran to the goal. On the remaining 9 control trials, Kanzi walked or ran to the goal and the uninformed person followed.

Figure 2 is a summary of the formal data. It may be seen that the starting point and goal location were different on almost every trial and the correct compass direction of travel varied among N, S, E, and W. Kanzi reached the goal on all 12 trials. Although we placed the goal object in the forest up to 48 h before a test was scheduled, and although Kanzi traveled in the forest before being given the cue, during the 12 trials Kanzi never started to go toward the object or found it until after he was given the cue. The mean time elapsed from the moment he was given a cue until he reached the goal was 16.9 min (range = 1–50 min), during which he sometimes stopped and ate parts of plants along the trail. Kanzi left the trail and made a shortcut through the woods toward the goal location during portions of Trials 1, 3, 4, 5, 7, 8, 11, and 12.

Figure 3 shows how Kanzi's distance from the goal varied as a function of how far he had traveled from the roadsign. Each of the dots on Fig. 3 is one data point out of the 6037 data points generated by digitizing Kanzi's 12 travel paths 6 times each. The data points fall into 12 distinct lines. Each line consists of the combined data from all 6 replications for one trial. Figure 3 shows that on 8 of the 12 trials, Kanzi's distance to the goal decreased steadily from the outset of the trial.

The median r-square between Kanzi's "travel distance so far" and his "straight-line distance now, from here to goal" for all 12 trials is 0.96. As the maps in Fig. 2 suggest, the lowest r-square, 0.08, came from Trial 11. The other r-squares ranged beween 0.78 (for Trial 4) and 0.9998 (for Trial 10). Even if the true N for purposes of significance testing is changed and assumed to be as small as 7 (5 degrees of freedom), 11 of the 12 r-squares are still statistically significant beyond the .01 level with a 2-tailed test. Alternatively,

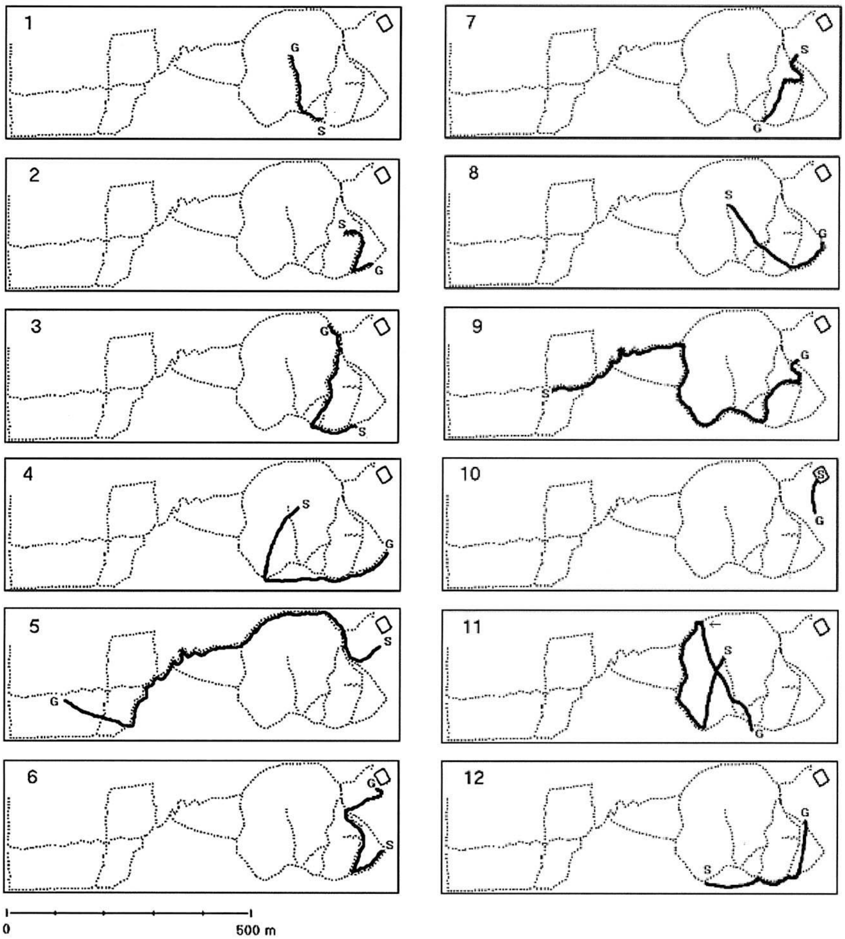

**Fig. 2.** Kanzi's travel routes in the 20-ha forest during the 12 control trials. S = start point at which he was given cue. G = goal location. Solid line = his path of travel. Dotted lines = human-made trails. The rectangle in the upper right is the laboratory building. The location at which Kanzi was given the cue a second time in Trial 11 is shown by an arrow.

an r-square of 0.96 with 12 degrees of freedom (one for each of our trials) is also highly significant.

It is obvious from Fig. 2 that Kanzi seldom if ever took the shortest possible path to the goal; the median D/MinD for the 12 trials is 1.46. Nevertheless, it seems equally obvious from Figs. 2 and 3 that Kanzi's paths were significantly distance-reducing overall, and usually so from the outset. Even on his worst trial (Trial 11), Kanzi headed straight to the goal after he was

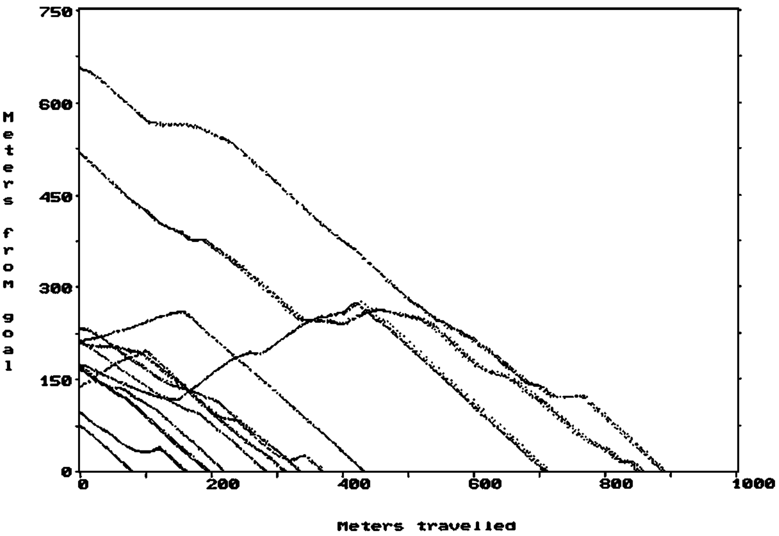

**Fig. 3.** Kanzi's distance from the goal during the 12 control trials as a function of how far he had travelled (total travel path length) after being shown the road sign. Each dot is one data point out of 6037 points generated by digitizing Kanzi's 12 travel paths 6 times each. Each line displays the combined data from a single trial.

given a second cue, and his starting move was not terrible either; he simply made an error in between, by taking one trail that went in a direction opposite to the correct direction.

Qualitative details of performance are equally interesting and important. For example, Trial 1 included the following notes by Savage-Rumbaugh: A new food location that contained mushrooms was established. Kanzi had been to the new location several times previously. The weekend caretaking staff knew nothing of the presence of mushrooms in the woods, nor did they have any idea that a new food site had been established. The caretaking staff was instructed to, at any point during the weekend when Kanzi seemed to be cooperative, ask him if he would take them to Mushroom Trail. They were instructed to follow him wherever he went. While at the A-frame, the weekend caretakers asked Kanzi to take them to Mushroom Trail. Kanzi immediately vocalized and started off down the main trail. When he passed the mushroom trail turn-off (an old drainage ditch joins this trail) he gestured to go down the drainage ditch. Normally, Kanzi was not allowed to wander far off the trails, and he was clearly taking a route that looked overgrown and not recently travelled. The caretakers hesitated in following Kanzi, thinking that perhaps he was using this as an opportunity to go into areas of the forest where he was not generally allowed to enter. However, after a brief discussion in which the caretakers recalled that their instructions were to follow Kanzi wherever he went, they decided to proceed. When the drainage ditch ended, Kanzi continued into the woods, and the caretakers followed, despite their later reports that they had thought nothing would be there. A short distance further, Kanzi discovered the first bag of mushrooms. Mushroom Trail was not a cleared or marked trail; it would not have been recognizable as a trail to an otherwise uninformed observer.

## DISCUSSION

There have been dozens of previous experiments conducted on primates (a few of them in the wild) and hundreds on other genera that convincingly demonstrate spatial memory in animals (Balda and Kamil, 1992). So what is new here?

A relatively unique aspect of our study was the use of arbitrary signs to designate varied distant locations at which a goal object would be found. The data strongly suggest that Kanzi used the information contained in a lexigram road sign to discriminate and to choose which distant location to visit. The spatiotemporal separations between the sign and the goal sites were also far greater than in previous studies of primate association learning, and the data reinforce previously expressed doubts as to the importance of spatial contiguity in learning (E. Menzel, 1974; Rumbaugh *et al.*, 1989). Whereas under some circumstances, in classical studies, separations of even a few cm or a fraction of a sec between a visual sign and a reward site might substantially impair performance, distances in our study ranged up to 650 m, travel times to the goal could exceed 15 min, and on most trials it was impossible for Kanzi to see the goal location from his starting location.

Latent learning is not a novel aspect of our study, but some readers might find this the most interesting aspect. Kanzi did not seem to require special, deliberate, persistent teaching or rewards on our part to learn about his environment. He showed his human caretakers things in the woods that they did not know themselves, and he appeared to be just as motivated to travel for nonfood rewards as for foods.

Another novel aspect of this study, as contrasted with previous experiments on animal spatial learning, is that the road sign was presented at different, arbitrary starting locations in a large-scale environment that could not be surveyed at a glance, and the positions of the experimentally-designated goals were also varied. In the control experiment, the starting places and the goals were virtually trial-unique, and they were presented at many different angles from one another. The significance of this procedure is that there was no apparent single environmental feature, such as the animal's home base, or the North Star, that could be used as a fixed reference point. The questions of what reference points, landmarks (Collett, 1996) or reference systems animals use, and whether and how the nervous system stores information about the global structure of the environment, are still of great interest today. The three major problems stated by Muller *et al.* (1996) and quoted in the Introduction are all aimed specifically at the issue of the structure or organization of spatial information. The significance of our study is that it directly addressed the first of these three problems and, of course, that Kanzi passed the test.

The two other types of behavior that have customarily been taken as evidence for generalized spatial knowledge—the ability to take novel shortcuts and ability to detour around novel barriers—have been more directly addressed in studies other than the present one. Nevertheless, Kanzi also demonstrated some instances of them. If he may be said to have passed all three tests at the same time, then that would be something new. Kanzi took shortcuts on numerous trials (Fig. 2). For example in Trial 5, he made one that was 175 m long. The shortcut was also novel for him, and it went through dense woods that he had never been allowed to enter. Along much of the shortcut, Kanzi could not see the goal location or any obvious landmark that was familiar to his human companions, and from the location where he began his shortcut, the goal location was not visible.

We did not introduce new barriers into the forest deliberately and experimentally, but some of them, e.g., flooding, fallen trees, snakes on the trail, occurred naturally over the course of the study. The most salient and interesting barrier has already been alluded to several times: for the most part Kanzi followed the trails (Fig. 2). The woods on either side of the trail were, however, not solid like the walls of a maze. The most substantial barriers here were probably habit, together with memory or immediate signs of what Kanzi's humans companions might do if he went where he was not supposed to go. Kanzi was as quick as any juvenile primate to detect when such socially-induced barriers were being raised or lowered, and he often varied his travel path accordingly (for example, qualitative notes cited on Trial 1).

Because Kanzi so often used the trails, his travel performance might underestimate his actual knowledge of goal directions. A question for future research is whether he and other apes can point toward any given goal location from any starting location, and whether they can point even while blindfolded or in an indoor room which permits no view of the outdoor environment (C. Menzel, 1999).

If it might be said that Kanzi passed all of the tests that Muller and coworkers (1996) and most proponents of cognitive mapping view as definitive, would this prove the case for cognitive mapping in animals, once and for all? Our guess is, probably not. The recent literature (Bennett, 1996), as well as the past, seems instead to illustrate that: “There is no single point at which all investigators will feel ‘forced’ to invoke cognitive concepts, and even individual thresholds in this regard are variable rather than constant” (E. Menzel, 1984, p. 524). The choice is whether to purge the term cognitive map from the language, as Bennett urges, or simply to assume cognitive mapping and take it for granted (and with a grain of salt), as Muller *et al.* (1996) and others (Kosko, 1986; Poucet, 1993) do, and to proceed from there. We are inclined toward the latter choice.

## What Is a Place, or a Place Name?

Our data do not resolve whether the lexigrams constituted place names or had any detailed geographical meaning for Kanzi. In some cases, however, it seemed clear that the signs signified particular objects and events that might be found or expected in a given location. For example, on Trial 62 of the first experiment, the road sign indicated to us that food was located at the dog pen. Unknown to us but known to Kanzi, the dogs that were usually housed there had been moved overnight to a new and different pen. The question was where Kanzi went—to the old place, with which this particular lexigram had been associated during the experiment, and which now contained food, or to where the dogs are now, a location at which Kanzi had never been given food, and for which he had not even been given a new lexigram. He went to the location where the dogs were at that time.

## What Was Learned?

The principal questions addressed in our study of spatial memory were: can Kanzi remember the locations of places that were not visible at the time of response? and on the basis of a sign, can he go from almost any arbitrary starting location to any goal location? These questions can be answered in the affirmative. The data suggest that in the 18 mo before the experiments began, Kanzi had acquired detailed knowledge of the human-made trail system if not the more general layout and structure of his large outdoor environment. He appeared to know where he was at any given time and also what leads to what (Tolman, 1938), for he could lead from any given place to almost anywhere else for which he and his human companions had a name. Casual inspection of our maps (Fig. 2) might suggest that the present trail system had relatively few choice points and was hence not very complicated compared to the mazes that rat psychologists used in the 1930’s. Nevertheless, we emphasize that much of the terrain was densely wooded with limited visibility, and that anyone not familiar with the same forest would sometimes find it hard even to identify what was a trail and what was not. The number of actual choice-points, landmarks, local signs and trail- and place-markers that Kanzi recognized and utilized at some time or another is not only unknown but probably unknowable, even in principle.

## Sign Learning

Miller and Dollard (1941) and E. Menzel (1973b) viewed the problem of leadership and communication as a special case of sign learning. The tasks in the present study required Kanzi not only to take over as the travel leader but also to assess at the very outset of a trial, from a discriminandum, which route to take and for which distant, nonvisible location to head. At the time of testing, Kanzi was still a juvenile. Assuming that bonobo developmental trajectories are similar to those of common chimpanzees, then at 4 years old while Kanzi was leading trips to the forest, his conspecifics in the wild would still be riding on their mothers' backs some of the time and sleeping every night in nests with their mothers. Furthermore, chimpanzee juveniles would still be a few years away from being relatively independent travellers when moving over substantial distances (Goodall, 1986; Kano, 1992). Before our experiments, nothing forced Kanzi to learn the network of trails that his mother surrogates had laid down and used, let alone to come up with novel shortcuts of his own, as he sometimes did. A sufficient strategy in the past was simply to follow or ride on the back of a caretaker.

Nevertheless, Kanzi behaved as if he recognized that the two lexigrams left on the post near his home cage provided information about the state of a distal location, and he guided or led his companions to the place designated by the lexigram. The motivation for a juvenile to be so independent is obscure, as the distances were huge by the standards of discrimination learning (Brown and Gass, 1993; Jarvik, 1953; Meyer *et al.*, 1965; Rumbaugh *et al.*, 1989), the directions were seldom a simple straight line, and there is nothing iconic or natural about a lexigram. A few footprints in the sand, or a broken stick pointing in a given direction, would be far more natural cues, but we know of no definite evidence to date that even an adult bonobo in the wild would use them (cf. Cheney and Seyfarth, 1985; Savage-Rumbaugh *et al.*, 1996). We would be surprised, however, if they could not do so, at least if sufficiently motivated and shaped. Might young bonobos learn the layout of their environments as well as Kanzi did even while riding on their mothers' backs? This seems less likely, but the possibility remains open.

The knowledge base of great ape navigation is still *terra incognita* compared to what is known about other species. We doubt that it is any less elegant or sophisticated. Partly for these reasons, our ongoing studies focus on what adult lexigram-competent chimpanzees can recall and later report about the places and things they have seen (C. Menzel, 1999).

The ultimate question posed by our study is probably this: If one had a suitable communication system to use with other animals, might one not find results just as remarkable as those shown by Kanzi? On the one hand, the communication systems that were used were relatively unique, and there is greater phyletic similarity between *Homo sapiens* and *Pan* spp. than between *Homo sapiens* and other species. On the other hand, some might argue that some animals already qualify, assuming that we learn their communication system rather than teach them ours. Data from social insects are particularly likely to be cited here. From this standpoint it is less a question of brain size or learning ability than a question of how animals make their livings, particularly as social beings and foragers.

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