The Organization of Exhaustive Searches in a Patchy Space by Capuchin Monkeys (Cebus apella)

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Search is a serial exploration of alternatives. Efficient search involves the ability to minimize costs (i.e., time/energy) and to keep track of alternatives already explored. The search abilities of 4 capuchin monkeys (Cebus apella) were evaluated by means of an apparatus featuring a set of suspended baited containers. The experiment featured conditions with different spatial configurations of the search space. Results show that the monkeys were able to search exhaustively 9 containers spatially distributed either as a 3 × 3 matrix or as 3 "patches" of 3 containers each. Search efficiency was higher in a search space suitable to organization in clusters or spatial chunks. In this condition, evidence for principled organization of search trajectories, as opposed to a random walk through the search space, emerges clearly and parallels search efficiency. This suggests that monkeys impose a structure over the search space and, by doing so, reduce the memory demands of the task.

In cognitive science, *search* is defined as the problem of what to do next in situations that require an exploration of multiple alternatives (Stillings et al., 1987). Implicit in this definition is the serial nature of search. The search space can be formed either by exteroceptive stimuli or by representations of objects, events, or problem states. Whatever the material on which it operates, the search process becomes a challenge for the cognitive system when the space of alternatives is large. In this regard, the vast variety of tasks, so often used in animal studies, featuring binary choices may be considered to be a trivial search problem (De Lillo, in press). In a binary situation, a random choice followed by a default strategy warrants the exhaustive exploration of the search space. By contrast, the serial exploration of a large number of alternatives requires the ability to keep track of the moves that the system is performing to avoid spending time and energy in reconsidering alternatives already explored. An obvious implementation of a nontrivial search task in the realm of animal behavior are tasks in which an animal has to explore a large set of loci, one after the other, in order to find items of food.

Following the pioneering work by Olton and Samuelson (1976), a vast amount of research has been conducted on rats running the radial maze. In a search space that affords strong spatial constraints, such as a radial maze, it is possible for the subject to deploy an algorithmic strategy consisting, for example, of visiting in succession adjacent arms following a particular direction of travel. This strategy would allow very efficient (no revisits) exhaustive searches without the need to remember each single location visited. Because the traditional focus of radial maze based research is the assessment of the memory span of the subjects, the degree of retention after a delay, and the type of memory code involved, the researchers have usually tried to devise tasks that cannot be solved by algorithmic strategies and, by contrast, require the subjects to rely on memory for depleted and not depleted food sites (e.g., Olton, 1982; Olton, Collison, & Werz, 1977; Olton & Samuelson, 1976).

A number of studies conducted on children suggest that the analysis of search strategies might prove to be informative regarding the cognitive status of the subject. The relative dependence of the performance on search strategies parallels cognitive development in children. Two-year-old children tested in the radial maze (Foreman, Arber, & Savage, 1984) perform marginally above chance and do not use any search strategy from the outset. Their performance contrasts with that of 4-year-old children, who rarely revisit previously explored arms and spontaneously deploy algorithmic strategies (such as making successive responses to adjacent arms). Moreover, the performance of 4-year-olds worsens when their use of search strategies is prevented. Therefore, it seems that older children rely more on strategies than on brute memory for the locations explored. This conclusion is supported by other results obtained with adult humans, 5- and 6-year-olds, and 1½-year-old children (Aadland, Beatty, & Maki, 1985). Here, an age-related trend was observed in both radial maze performance and in measures of the sequential organization of search, such as (a) entering four arms in sequence in the first 4 choices, (b) the probability of starting to search from a fixed location, (c) the tendency of moving to adjacent arms, and (d) the consistent use of a fixed travel direction. When the use of principled search patterns was prevented, older children and adults worsened in their performance, whereas the accuracy of 1½-year-olds remained unaffected.

If much is known about the spatial memory of rodents and the cognitive relevance of strategic search in human devel-

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opment, relatively little work has been done on the performance of primates in spatial tasks that allow one to investigate search strategies. In studying the relationship between memory and search behavior in chimpanzees, Menzel (1973) showed that they are able to remember most of the hiding places of food items within a large outdoor enclosure, that they economize travel distance, and that the frequency of repeated visits to locations already explored is practically negligible. However, in nearly half of the trials (11/24 = 46%), chimpanzees failed to retrieve exhaustively four pieces of food (the average number of retrievals is not reported in the study when, in full view of the subject, they were dropped in the grass and were not "covered up further" (Menzel 1973, Experiment 4), suggesting that their performance relied strongly on cues inevitably left by unburying the food. More recent studies have shown yellow-nosed monkeys (Cercopithecus ascanius whithesidei; MacDonald & Wilkie, 1990) and gorillas (Gorilla gorilla gorilla; Mac-Donald, 1994) performing exhaustive searches of a set of eight cups covering food items. In performing exhaustive searches, monkeys were shown to avoid revisits to previously depleted food sites (McDonald, 1994). However, here too, the interpretation of the results is ambiguous. In fact, the procedure adopted is restrictive because of the displacement of the cups at each choice that leaves a permanent trace of each location visited. Therefore, data concerning exhaustive searches in nonhuman primates are flawed by the particular setup used, which provides unequivocal cues for locations visited. Yet, a measure of reiterations is essential for properly evaluating the ability of primates to keep track of moves made over time.

In a study conducted on common marmosets (Callithrix jacchus jacchus), MacDonald, Pang, and Gibeault (1994) modified the task used by MacDonald and Wilkie (1990) and MacDonald (1994) by using containers that could not be displaced by the monkeys. Therefore, this study provides information about the ability of the monkeys to keep track of the sites explored in the absence of external cues. The study featured three experiments testing accuracy in a free foraging situation, in a win–stay and a win–shift task, respectively. In the free foraging situation, the marmosets searched exhaustively a set of eight containers in most of the trials administered, and their accuracy (measured as the number of containers visited in the first 8 choices) was above chance. The movement of the monkeys across the search space was not regular, suggesting that monkeys relied mainly on memory to avoid revisiting depleted sites. Monkeys had, on the other hand, preferred starting positions and these coincided with the closest locations to their release site. The one subject tested in Experiment 2 and the two subjects tested in Experiment 3 for the ability to remember a subset of four randomly chosen sites according to a win–stay or a win–shift task, respectively, chose adjacent locations in successive correct choices.

For the study of memory and search in primates, we devised an apparatus on which no visible cues were present for visited locations, which allows a flexible manipulation of the spatial structure of the search space and, instead of preventing them, focused our analyses on the organization of the search patterns of our subjects. The task is an exhaustive search within a set of multiple locations. The monkey is presented with a set of containers suspended on the ceiling of the cage and has to explore them serially to retrieve hidden food. The aim of this study was to evaluate the effects produced by the spatial configuration of loci to be explored on the search economy of the monkeys. In particular, we compared, using a within-subjects design, a configuration of stimuli characterized by a diffuse distribution of the loci within the set and a configuration characterized by the presence of spatial clusters.

Our working hypothesis was that a search space organized in clusters, if explored in a principled manner, should provide the subjects with the possibility of chunking it spatially (first visiting each location within the same clusters and then moving to another cluster). This, in turn, should reduce the number of items of which the subject has to keep track, and of the number of clusters that are progressively explored, instead of the total number of loci composing the set.

In nonprimate species, there are a number of studies aimed at investigating the relationship between the structure of search space and the economy of search by manipulating the spatial arrangements of the arms of radial mazes (Phelps & Roberts, 1989; Roberts, 1979, 1984; Roberts & Ilerish, 1989). These studies have repeatedly shown that the spatial structure of the search space plays an important role in determining performance. Rats, for example, show a very high accuracy of choice (measured in terms of redundant moves to arms already visited) in mazes the spatial structure of which supports a hierarchical organization of search (Roberts, 1979, 1984). Rats benefit also from qualitative clustering of food items (Dallal & Meck, 1990). Nevertheless, chunking in rats seems to be a strategy of only relative robustness because there are situations in which they worsen their performance as a function of the angular relationship among the arms of a radial maze (Shenk, Contant, & Grobety, 1990).

Under different conditions, chunking has recently been observed among rhesus monkeys (Macaca mulatta) facing a serial learning task (Swartz, Chen, & Terrace, 1991). Within serial learning studies, capuchin monkeys (Cebus apella) have been used extensively as experimental subjects within experiments not directly focused on chunking (e.g., D'Amato & Colombo, 1988, 1989). Serial learning experiments on capuchins represent an important background for the present study because they have demonstrated that this species, in contrast with pigeons, form an ordered representation of the series they learn. Therefore, capuchins are appropriate subjects for a study aimed at investigating the relationship between serial organization, search economy, and memory. Serial learning tasks are designed to prevent the subjects from organizing sequences of responses on the basis of the spatial arrangement of the stimuli. In these studies, the sequence of items to be reported is chosen on an arbitrary basis, and strict training procedures are used. Apart from a few exceptions (e.g., Terrace, 1987), the material presented to the subjects does not afford either relational or

categorical properties of the stimuli (for a methodological review of the paradigm, see De Lillo, in press).

The complementary line of enquiry that we decided to follow was to leave the animal completely free to organize its own serial behavior in the presence of a problem with strong serial components, a demanding task for the memory system, and where there was an opportunity to search in a principled manner on the basis of the spatial relationships of the configuration of loci to explore. In this manner, we aimed to identify the spontaneous emergence of order as a data-reducing device in a task that was potentially demanding for the memory system.

Method

Subjects

The subjects were four capuchin monkeys (*Cebus apella*): a captive-born female 12 years of age (BR); a wild-born male, approximately 5 years of age (NA); a captive born male, 4 years of age (PA); and a wild born female approximately 5 years of age (VI). All the monkeys were socially housed at the Institute of Psychology of the Consiglio Nazionale delle Richerche. Each subject was separated from the group only for the testing just before each daily testing session. This procedure was not stressful for the animals and did not disrupt the behavior of either the separated individual or its group mates. Subject BR had been used in a variety of experiments in the past, however, none of the experiments was based on search tasks. All the other subjects were experimentally naive.

Apparatus

The experiment was conducted in a squared cage (3 m wide × 2.50 m high). Three walls of the cage were made of concrete and the floor of concrete and metal bars. The fourth wall and the ceiling were made of wire mesh. In each of the three concrete walls, a guillotine door was installed. On the three walls with no wire mesh, a perch of the same length of the wall allowed the monkey to reach the ceiling of the cage easily. The cage was illuminated by a fluorescent light from above the ceiling. Therefore, many landmarks were provided to the monkeys by the asymmetrical features of the cage. Nine opaque plastic containers were suspended by means of a metal chain about 5 cm long, hooked onto the ceiling. The containers were identical in shape (cylindrical), size (diameter, 3 cm; depth, 2.5 cm) and color (grey). A reward (half a peanut) was hidden in each of the nine containers. This arrangement allowed the monkeys to recover the reward easily and prevented a view of the reward from any point of the cage. The subject could check whether a container was full or empty only by manipulating it.

Procedure

Before a trial started, all nine containers were baited, in the absence of the subject. During the baiting procedure, the subject was kept in one of two enclosures (waiting cages) situated on the side of the experimental cage. Each waiting cage was connected to the testing cage by means of a guillotine door. The waiting cage in which the subject was kept before each trial was selected according to a pseudo-random procedure to prevent the subject from entering the testing cage from the same side on more than two

consecutive trials. After completion of the baiting procedure, the guillotine door was lifted and the subject entered the testing cage and was permitted to search the containers to retrieve the baits. The exit of the subject from the experimental enclosure was achieved by reopening the guillotine door, either after it had visited all the containers (exhaustive search) or after 15 min had elapsed, whichever occurred first. An interval of 3 min was interposed between successive trials, during which the containers were rebaited. Each daily experimental session consisted of five trials; 25 warmup trials were administered to familiarize the subject with the testing setting and the task. The experimental design featured three conditions: a baseline condition, an experimental condition, and a control condition. Each condition consisted of 60 trials. For each condition, the spatial arrangement of the set of containers was manipulated as follows.

Warmup trials. The spatial arrangement of the containers was a 3 × 3 matrix. The distance between two adjacent containers was of 70 cm within a row or a column (see Figure 1a).

Baseline condition. The spatial arrangement of the containers was the same as for the warmup trials: a 3 × 3 matrix with a distance of 70 cm between two adjacent containers (see Figure 1a).

Experimental condition. The distance between the containers was manipulated to form three spatial clusters of three containers each (see Figure 1b). The distance between the containers within a cluster was 35 cm. The minimal distance between containers belonging to different clusters was 110 cm.

Control condition. The spatial arrangement featured in the baseline condition was reestablished to control whether effects
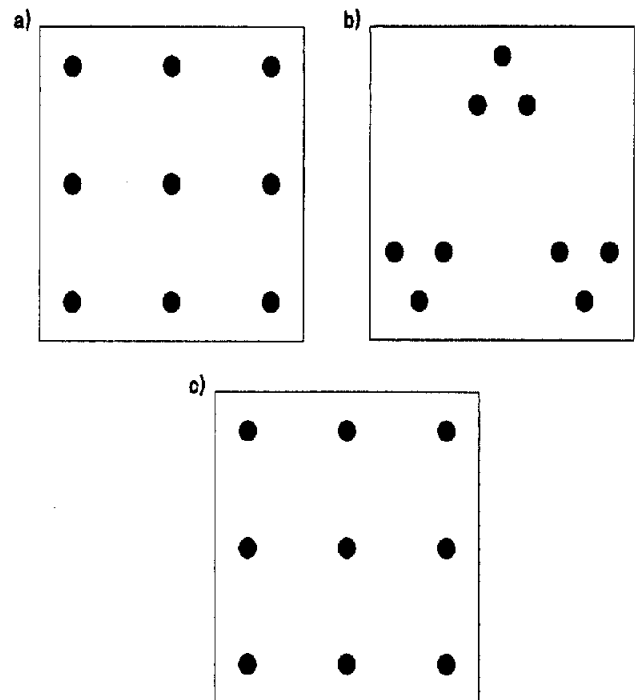

Figure 1. Scheme of the spatial configurations of the search space used for (a) baseline condition, featuring an arrangement of containers according to a 3 × 3 matrix; (b) experimental condition, featuring a patchy search space in which the containers are arranged according to three spatial clusters; and (c) control condition, in which the configuration of the baseline condition is represented in order to control for a general effect of task practice.

attributable to the experimental condition could instead be due to mere task practice.

Data recording. Each visit to a container (defined as the subject touching the container with a hand), the spatial position of the container, and the serial order of each visit were recorded on a check sheet.

Results

Spontaneous Deployment of Exhaustive Searches

The procedure proved to be effective from the start because, in the warmup trials, the subjects began to search the containers spontaneously as soon as they were introduced into the experimental cage. Moreover, searches were exhaustively completed in the vast majority of trials before the 15 min allowed had elapsed: BR 21/25, NA 25/25, PA 20/25, and VI 21/25, $\chi^2(3, N = 4)$ 28.56; $p < .001$. In the baseline condition, BR performed exhaustive searches in 53 trials out of 60; NA, in 60 trials out of 60; PA, in 55 trials out of 60; and VI, in 58 trials out of 60, $\chi^2(3\ N = 4)$ 94.6; $p < .001$. In the experimental and in the control conditions, all the searches performed by the subjects were exhaustive.

Search Efficiency

Analysis of the efficiency of search was conducted on those trials during which an exhaustive search was accomplished. Warmup trials were excluded from the analysis. The number of moves performed in each trial was analyzed by means of a mixed-design analysis of variance: Subject (4) × Condition (3) × Blocks of Trials (6). No overall differences emerged among the subjects. By contrast, a significant difference emerged among conditions, $F(2,$

$64) = 39.99$, $p < .001$. As shown in Figure 2, there was a dramatic decrease in the average number of moves in which searches were completed in the experimental condition.

Post hoc comparisons showed that the number of moves per trial observed in the baseline condition and the experimental condition ($p < .001$) and between the experimental condition and the control condition was statistically different ($p < .001$). A statistically significant difference was also observed between the baseline condition and the control condition ($p < .01$). Nevertheless, as may be seen in Figure 2, this latter difference was less evident than the difference observed between the experimental phase and both the baseline and the control condition.

Post hoc comparisons between conditions were performed for each of the subjects. For all the subjects, a significant difference emerged between the experimental and the baseline conditions (BR, $p < .05$; NA, $p < .01$; PA, $p < .001$; VI, $p < .001$), whereas the difference between the experimental and control conditions was significant for only 3 of the 4 subjects (BR, $p < .001$; NA, $p < .01$; VI, $p < .05$). The behavior of subjects BR and NA confirmed the hypothesis that no difference should emerge between the baseline and the control conditions. In fact, for these 2 subjects, the post hoc test conducted on the baseline and the control conditions did not yield statistical significance. By contrast, some effects of transfer of learning between conditions was observed for the other 2 subjects that improved their economy of search moving from the baseline to the control condition (PA, $p < .01$; and VI, $p < .01$).

For each of the subjects, the experimental phase is characterized by a decrease in the number of moves compared with the baseline and the control conditions (Figure 2). Such a decrease is explained by a shift in the distribution of trials
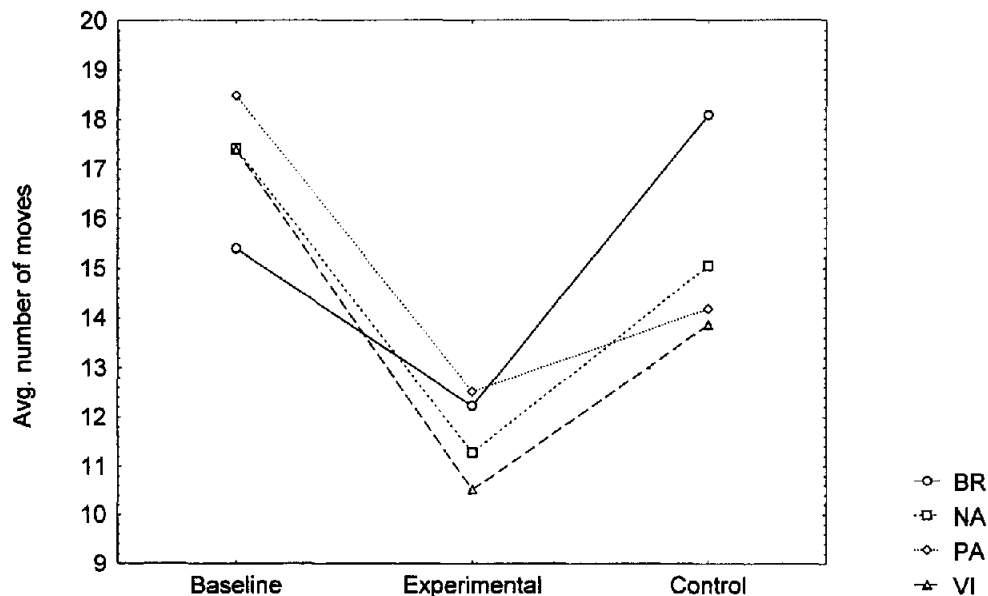

Figure 2. Average (Avg.) number of moves in which exhaustive searches were completed by each subject (BR, NA, PA, VI) in the baseline, experimental, and control conditions.

toward the trials characterized by a minimal number of moves (9 moves) as shown in Figure 3.

The change in the form of the distribution of the trials from the baseline to the experimental condition was evident for all the individuals. However, for BR and NA (which showed a significant increase in the number of moves in the control condition as compared with the experimental condition), the distribution of trials in the control condition mimics more closely the form observed in the baseline condition than for PA and VI, which did not affect their economy of search in the control condition.

Effects of Task Practice

An analysis of the trend in the number of moves performed on the six different blocks in which each of the conditions was divided showed that, in the experimental condition, the group of subjects practicing the task reduced the number of moves according to a linear component, $F(1, 32) = 15.70$ $p < .001$. On an individual basis, 2 of the subjects showed a significant trend in this phase: NA, $F(1, 32) = 6.20$ $p < .05$; PA, $F(1, 32) = 7.27$, $p < .05$. By contrast, the trend was not significant in the baseline and in the control conditions for the group of subjects as a whole and for each of the individuals. The average number of moves used by each subject to perform an exhaustive search of the nine containers in each block of trials is reported in Figure 4.

Modes of Search: Evidence of Behavioral Organization

A search task such as the one used here offers the possibility of evaluating the emergence of forms of spontaneous organization of behavior, in the absence of any explicit training. In fact, in this task, one could expect the behavior of the animals to fall along a continuum ranging from a massive use of working memory (in the absence of any organization of the search path in the configuration to be explored) to the use of principled paths through the search space. Once the path is stored in long-term memory, search would require virtually no use of working memory at all. Therefore, to assess where the behavior of the monkeys was to be positioned along this continuum, we conducted an analysis of the transitions performed by the subjects from and to each of the loci explored while searching. If subjects relied mainly on working memory, in the absence of behavioral organization, we should expect a transition frequency matrix in which observed values fill the cells at random according to the conventional formula (see Van Hoof F, 1982)

$$e_{ij} = (o_{i*} \times o_{*j})/o^{**},$$

Where e_{ij} is the expected value for a given cell, o_{i*} is the total of the row's total, o_{*j} is the column's total, and o^{**} is the general total.

We used the χ^2 test (1 df) to compare the observed values
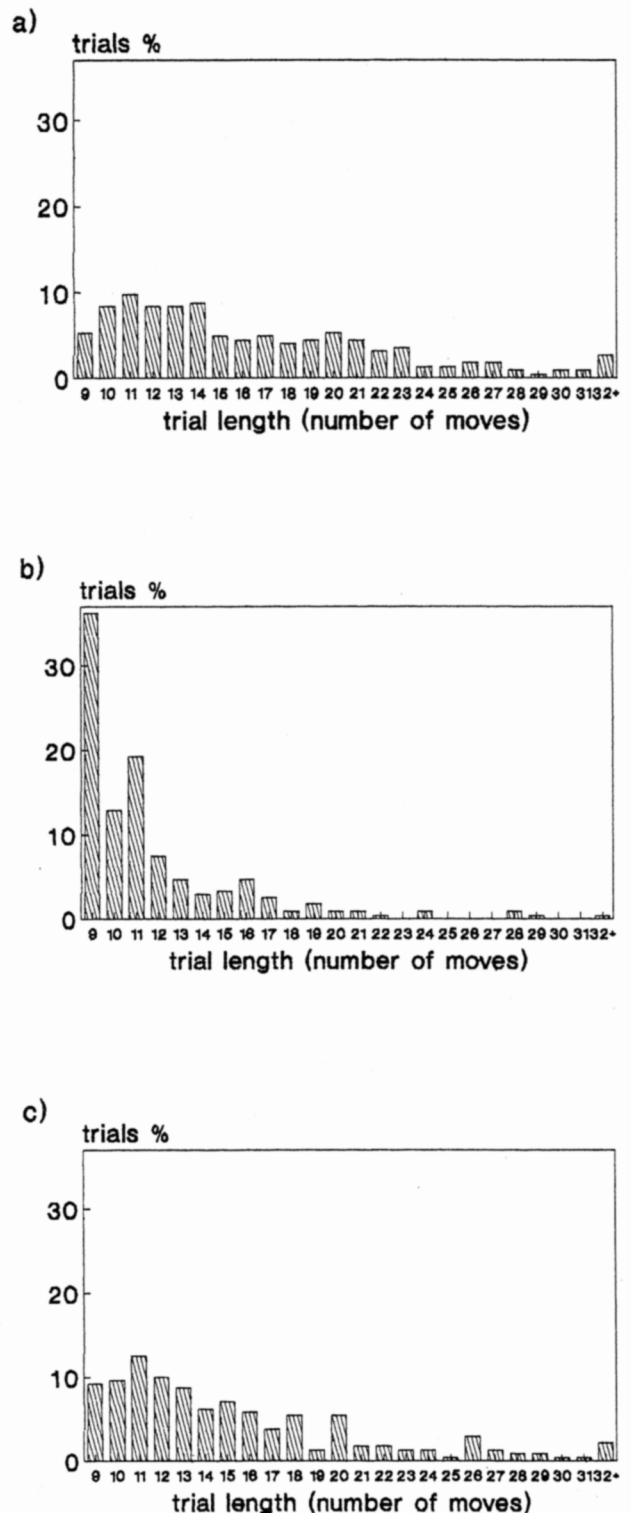

Figure 3. Distribution of trials characterized by a particular search length (measured in terms of the number of moves in which they were completed) obtained in the (a) baseline condition (matrix); (b) experimental condition (clusters); and (c) control condition (matrix) for the group of subjects.
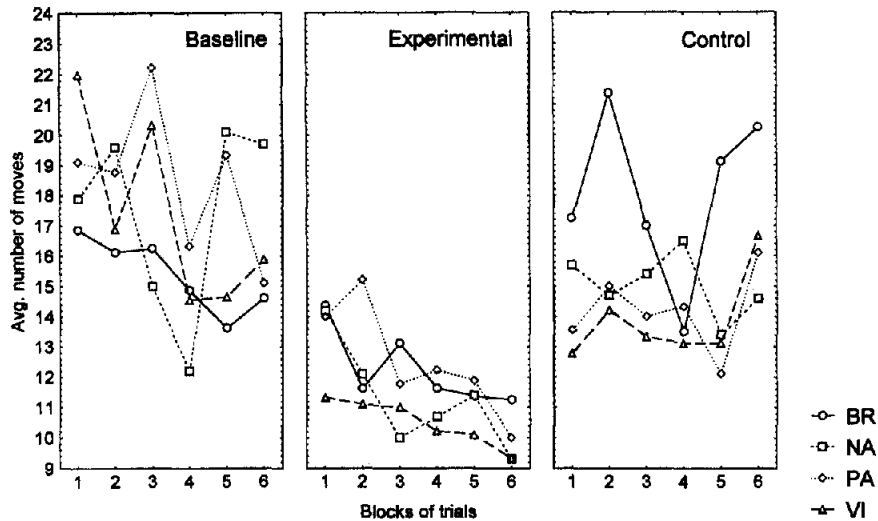
Figure 4. Average number of moves performed to complete a search in successive blocks of trials (each consisting of 10 trials) by each subject (BR, NA, PA, VI) in the baseline, experimental, and control conditions.

for each transition with those expected by chance. We also checked whether subjects had a tendency to begin and end the search in particular positions by means of χ^2 (1 *df*) performed on the first and the last move of the subjects (comparing the observed frequencies with those expected if the subjects were selecting at random between all the nine loci). The results obtained for each of the conditions and for each of the individuals are reported in Figure 5 as pathway diagrams.

Figure 5 shows that not all the transitions were performed significantly above chance and that the subjects had preferred starting and ending points. It is also evident that subjects used a minimal distance principle while moving from one container to the next. In fact, transitions are performed almost exclusively between adjacent containers. The thickness of the lines in Figure 4 also indicate that some of the transitions observed above chance were performed more than others. Thus, monkeys did not follow random trajectories while searching. However, strong individual differences can be noted.

Evidence for Spatial Chunking

To use a "patchy" configuration effectively (as a memory aid) a subject should explore exhaustively each of the clusters before moving to the next. By doing this, it would have only three items to remember at a time (the three loci within a cluster) and then the position of the three clusters. By contrast, a subject that does not follow this rule should remember each individual position of the nine containers composing the set (to avoid reiterations on loci already explored when it reenters a cluster explored only partially).

An analysis of the errors performed in the experimental condition allows the assessment of whether the subjects used the spatial constraints afforded by the "patchy" search

space in such a principled way. All the errors performed by the subjects were scored and classified as (a) intracluster error, that is, the revisiting of a container located in the same spatial cluster of the container visited immediately before; (b) extracluster error, that is, revisiting a container located in a spatial cluster different from the one visited immediately before. Both intra- and extracluster errors were then divided into (a) error type 1/3, where only one container out of three had already been visited within the cluster in which the error occurred; (b) error type 2/3, where two containers out of three had already been visited within the cluster in which the error occurred; (c) error type 3/3, where the cluster in which the error occurred had already been exhaustively visited. The observed frequencies of intracluster errors included 25 errors type 2/3 and 118 errors type 3/3. The observed frequencies of extracluster errors consisted of 9 errors type 1/3, 83 errors type 2/3, and 392 errors type 3/3. These data show that the vast majority of errors observed consist of visiting a container within a cluster that had already been exhaustively explored (errors type 3/3) and that most of these sort of errors were performed when moving from one cluster to the next (extracluster errors). In other words, the subjects found the identification of entire clusters not yet explored difficult. By contrast, it was relatively easy for them to remember the loci explored within a cluster.

The existence of a relationship between the use of a principled trajectory through a patchy search and the ability to keep track of the loci already explored is further supported by the analysis of the relationship between the frequencies of exits from a cluster not already exhaustively explored (i.e., neglecting some items) and the frequencies of errors performed by reentering the cluster and visiting empty containers (those that had been explored before leaving the cluster). If the subjects' performance is dependent on
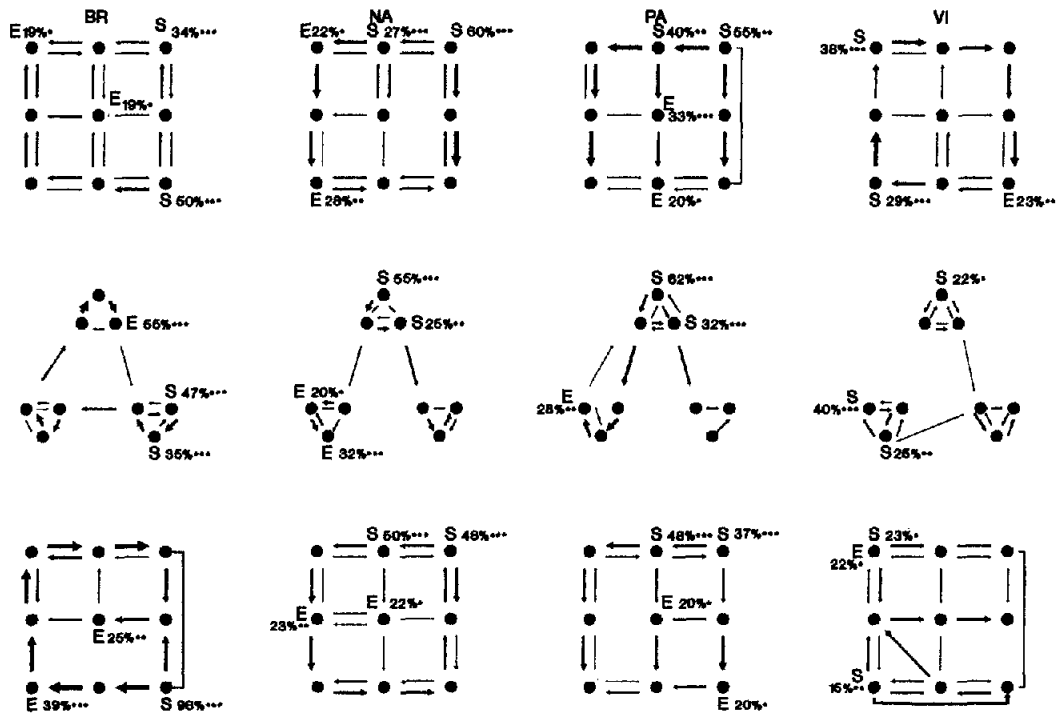
Figure 5. Transitions performed between successive moves within the search space by each subject (BR, NA, PA, VI) and preferred search starting and ending points. From top to bottom: baseline, experimental, and control conditions. Only statistically significant transitions are reported as arrows. The thickness of the arrows is proportional to the observed frequency of the transition. Only search starting and ending points selected above chance level are reported. S = preferred starting positions; E = preferred ending positions. For each starting and ending point, the percentage of trials in which that particular location was observed to be a starting or ending point is reported. Asterisks indicate the level of statistical significance: $*p = .05.$ $**p = .01.$ $***p = .001.$

the organization of search, we should expect the two measures to be correlated because the subjects would not be able to keep track of locations when the hierarchical organization is disrupted. By contrast, if the subjects rely merely on brute memory, the two measures should prove to be independent because the subject would remember each container regardless of its belonging to a particular spatial cluster. When the correlation between the frequencies of exits and the frequencies of errors for each block of trials has been tested, a high parallelism between the two measures emerged (Pearson's product–moment $r = .95$).

Moreover, a trend analysis showed a strong linear component in both the reduction of the frequencies of errors, $F(1, 3) = 18; p < .02,$ and the number of exits from a cluster before its completion, $F(1, 3) = 20; p < .02.$ This latter result shows that the organization of search behavior is not induced by the characteristics of the configuration from the outset. On the contrary, it seems to develop in parallel with the acquisition of expertise with such a search space as that featured in the experimental condition (it is only in the experimental condition that a trend can be observed in search efficiency and that decreased accuracy in the control condition rules out a major effect of task practice transversal to the shape of the search space).

Discussion

In the present study, we developed and tested an apparatus that allows the study of primate's search behavior in conditions in which no physical trace is left for choices already made. This allowed us to show that monkeys are able to perform exhaustive searches within sets of nine loci, in conditions in which the subjects have to keep track (either by memorizing or by organizing principled search patterns) of the loci already explored in each trial.

By manipulating the spatial configuration of the search space, it was possible to show that capuchin monkeys produce less redundant moves when searching a patchy configuration as compared with the baseline condition featuring a 3 × 3 matrix of loci. Moreover, for two monkeys, a significant increase in the number of redundant moves was also observed when, after having being presented with the patchy search space, they were retested in a control condition identical to the baseline condition. A similar increase was observed in the remaining two subjects, although for them the increase in the number of redundant moves in the control condition was not significant. Therefore, the positive effects on search efficiency have to be accounted for by the form of the search space and only to a lesser degree by

a general effect of task practice. Nevertheless, task practice plays a major role in the efficiency level reached while searching the patchy search space.

The fact that monkeys performed exhaustive searches (a requirement not always met in previous studies) was an important precondition for the assessment of the presence of cost evaluation functions related to search efficiency. In fact, we were able to assess whether, in the presence of an overall success (collecting in every trial all of the available items of food), capuchin monkeys used other sources of feedback (such as time or energy spent searching) to regulate their behavior further. Behavioral regulation was observed in the condition featuring a patchy search space during which a positive trend in the reduction of redundant moves was observed. Therefore, it seems that capuchin monkeys are able to monitor the costs associated with each redundant move and use this information to regulate their behavior. Nevertheless, this ability is restricted to situations in which the set of loci, for the spatial constraints that it affords, allows spatial chunking.

The fact that the performance of monkeys was associated with the organization of principled search trajectories was evident from the analysis of transitions performed from and to each location. Subjects proved to search in a nonrandom fashion. The relationship between chunking and performance was also evident from analyses showing that (a) extracluster errors occurred more frequently than intracluster errors; and (b) exiting a cluster before it is exhaustively searched (neglects) predicts errors when the cluster is reentered.

It has been pointed out that an important dimension in cognitive development (Brown and Deloache, 1978; Flavell and Wellman, 1977) and in comparative cognition (McGonigle, 1984) is the extent to which an organism is able to individuate, on the one hand, the limitations of its cognitive resources and, on the other, the relevance of using strategies in a variety of tasks. In this regard, the difference that we observed in capuchin monkeys between the patchy and the diffuse search space conditions might be the expression of the ability of primates to exploit the constraints afforded by the particular problem they face. In this case, the effect that we observed in the search behavior of the monkeys might be produced by their strategic use of the spatial structure of the search space. If this is true, we should expect these subjects to perform equally well on any other highly structured configuration. On the other hand, studies conducted within the behavioral ecology perspective have often emphasized the need to consider modes of search as a function of the particular diet of a species and as a consequence on the distribution of a particular food resource. Often, these studies are conducted on avian species (e.g., hummingbirds: Cole, Hainsworth, Kamil, Mercier, & Wolf, 1982), however, the same emphasis on the relationship between diet and search mode could be put in the interpretation of our results with monkeys performing a task that closely resembles a foraging situation.

The finding that monkeys' search efficiency is best expressed in a patchy search space could be interpreted as evidence for a specialization of capuchin monkeys for for-

aging in patchy environments. Indeed, it has been proposed that the evolution of intelligence in primates originates in their frugivoriness (and therefore the need to forage on patchily distributed resources; Milton, 1981, 1993). This hypothesis could be tested in a comparative study. In fact, different primate species are frugivorous to different degrees (Guillotin & Sabatier, 1994). For example, within New World monkey species, spider monkeys (*Ateles paniscus*) are almost exclusively frugivorous, howler monkeys (*Alouatta spp.*) are almost exclusively leaf eating, whereas capuchin monkeys (*Cebus apella*) are frugivorous and partially insectivorous. Thus, if the ability to explore a patchy environment is to be accounted for mainly by a cognitive specialization of a frugivorous species, we should expect a great difference of search efficiency in patchy and diffuse search spaces in spider monkeys. In howler monkeys, by contrast, the difference should be less evident. The value of the difference between the results that we obtained in the two conditions with capuchin monkeys should fall somewhere between those observed in the other two species.

In the light of our results and of those obtained in developmental (see Aadland et al., 1985; Foreman et al., 1984) and comparative studies (McGonigle, De Lillo, & Dickinson, 1992; Terrace & McGonigle, 1994; Visalberghi & De Lillo, 1995), we would favor the hypothesis that a wide variety of primate species, by virtue of their cognitive sophistication, are able to detect the spatial affordancies of different search spaces and, as a consequence, to impose a structure over material that, by contrast, remains relatively unstructured for simpler organisms. Whatever the theoretical approach favored, the organization of search might prove a dimension of comparative relevance and provide affluent information on the relationship between specialization, flexibility, and the evolution of cognition.

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