

Spatial Constraints and Regulatory Functions in Monkeys' (*Cebus apella*) Search

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By means of an apparatus featuring a set of suspended baited containers, search abilities of 4 capuchin monkeys (*Cebus apella*) were evaluated. The experiment featured different spatial configurations of the search space. Results showed that monkeys exhaustively searched 9 containers spatially distributed as a 3×3 matrix, a cross, a line, or a circle. Search efficiency was higher when the search space featured either a linear or circular arrangement of containers. When faced with a linear arrangement of containers, the subjects developed principled search trajectories from 1 end to the other of the linear array. This behavioral regulation was independent from search efficiency as measured by the amount of visits to containers already explored. The data suggest that monkeys use either the travel distance or the cognitive costs associated with unprincipled travel trajectories as currency for regulation.

Tasks involving the exploration of a set of baited sites have been widely used in animal cognition research. Most of the studies after Olton and Samuelson (1976) have focused on rats running a radial maze and the assessment of their spatial memory (i.e., memory for locations). The radial maze affords strong spatial constraints, and, as such, a rat running the maze can deploy an algorithmic strategy consisting of, for example, visiting adjacent arms in succession following a particular direction of travel. This strategy allows very efficient (no revisits) exhaustive searches without the need to remember each single location visited. Researchers interested in brute memory span have considered the ability to use such a strategy (or indeed any other that minimizes the memory demands of the task) as a spurious variable, and they have devised special procedures to control it (e.g., forced choices, Olton, 1982; Olton, Collison, & Werz, 1977; Olton & Samuelson, 1976).

Nevertheless, the ability of an organism to find computationally simple strategies to solve tasks that are otherwise demanding in terms of information management might be in itself an indicator of that organism's cognitive status (Terrace & McGonigle, 1994). Radial-maze-based studies of human cognitive development indeed show that the relative dependence of performance on search strategies parallels cognitive development. Two-year-old children perform marginally above chance and do not use any search strategy (Foreman, Arber, & Savage, 1984). In contrast, 4-year-old

children rarely revisit previously explored arms, they deploy algorithmic strategies, and their performance worsens when the use of strategies is prevented. Therefore, older children seem to rely more on strategies than on brute memory to identify the locations explored. This conclusion is supported by other results obtained with adult humans, 5- to 6-year-olds, and 18-month-old children (Aadland, Beatty, & Maki, 1985). Here, an age-related trend was observed both in radial maze performance and in measures of the sequential organization of search, such as (a) entering four arms in sequence in the first four choices, (b) the probability of starting to search from a fixed location, (c) the tendency to move 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 the 18-month-old children remained unaffected.

Researchers who study nonhuman primates have addressed the issue of spatial memory, and they have described some components of search patterns. Chimpanzees (Menzel, 1973) searching for hidden food items within a large outdoor enclosure economized traveling distance and avoided repeated visits to locations already explored. Yellow-nosed monkeys (*Cercopithecus ascanius whitesidei*; MacDonald & Wilkie, 1990) and gorillas (*Gorilla gorilla gorilla*; MacDonald, 1994) efficiently searched a set of eight cups covering food items. A study on common marmosets (*Callithrix jacchus jacchus*), (MacDonald, Pang, & Gibeault, 1994) showed, among other things, that in a free-foraging situation the marmosets exhaustively searched a set of eight containers in most of the trials administered, and their accuracy (measured as the number of containers visited in the first eight choices) was above chance. In this latter study, the movement of the monkeys across the search space was not regular, suggesting that monkeys mainly relied on memory to avoid revisiting depleted sites. The marmosets had, nevertheless, preferred starting positions that coincided with the locations closest to their release site. Moreover, some evidence was presented regarding the preference of the

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monkeys for moving to adjacent locations in successive correct choices.

The immediate background of the experiment reported here is a previous study (De Lillo, Visalberghi, & Aversano, 1997) specifically designed to investigate the effects of the spatial structure of the search space on the economy and the organization of tufted capuchin monkeys' (*Cebus apella*) search. The study was conducted using a suspended set of baited containers so that no physical trace was left for choices already made (see De Lillo & McGonigle, in press, or De Lillo et al., 1997 for comments on this issue). In that study, it was found that monkeys are able to perform exhaustive searches within sets of nine loci under conditions where the subjects have to keep track (either by memorizing or by organizing principled search patterns) of the loci already explored in each trial. Capuchin monkeys produced less redundant moves when searching a hierarchical spatial structure formed of three clusters of three loci each as compared with conditions featuring a 3×3 matrix of loci.

Moreover, that study (De Lillo et al., 1997) showed that in the presence of an overall success (collecting all of the available items of food in every trial), capuchin monkeys, in the course of task practice, spontaneously reduced the number of visits to containers already explored. The authors proposed that capuchin monkeys are able to monitor the costs (in terms of time and/or energy spent searching) associated with each redundant move and use this information to regulate their behavior. Nevertheless, this ability seemed to be restricted only to a situation in which the set of loci, for the spatial constraints it afforded, allowed spatial chunking. Two possible interpretations of this finding were proposed.

Following theoretical frameworks that consider 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, in a variety of tasks, strategies that allow better information management (Flavell & Wellman, 1977; Brown & DeLoache, 1978, for a discussion in the context of cognitive development; McGonigle, 1984, for a discussion in the context of comparative psychology), De Lillo et al. (1997) proposed that the increase in search efficiency in the presence of a configuration that allowed spatial chunking could have been produced by a strategic use of the spatial constraints afforded by the search space.

If this proposal is true, researchers should expect capuchin monkeys to perform equally well on any other highly structured configuration that does not feature spatial clusters but nevertheless affords other data-reducing strategies different from spatial chunking. For instance, a subject exploring a linear array of containers, if it starts from one end point and moves on to adjacent locations without changing its direction of travel, can avoid redundant moves without having to remember which containers have already been visited (see De Lillo, 1996). The spatial structure of the search space itself will act as a sort of notational system that, as a function of the position of the subject, will tell it unambiguously which loci have been depleted and where to search next. In contrast, a random search would require the subject to remember the locations explored or those that have yet to be explored or both.

An alternative hypothesis comes from studies that emphasize the need to consider modes of search as a function of the particular diet of a species and as a consequence of the distribution of a particular food resource. Often these studies are conducted on avian species (e.g., hummingbirds; see Cole, Kamil, Hainsworth, Mercier, & Wolf, 1982). However, the same emphasis on the relationship between diet and search mode could be applied to the interpretation of results obtained with monkeys performing a task that closely resembles a foraging situation. The finding that monkeys' search efficiency is best expressed in a search space formed by a cluster of items could be interpreted as evidence for a specialization of capuchin monkeys (whose diet is mainly frugivorous, Guillotin & Sabatier, 1994) for foraging in patchy environments. This interpretation, however, would apply mainly to search spaces featuring spatial structures that closely match natural foraging conditions (such as a set of spatial clusters resembling the patchy distribution of fruit) and would apply less to different configurations that allow a principled search but less closely resemble the distribution of natural resources.

The present study aimed at (a) evaluating the extent to which capuchin monkeys are able to efficiently search different spatial configurations of nine loci characterized by strong linear and circular components; (b) assessing the effects produced by the manipulation of the spatial structure of the search space; (c) detecting, if any, the qualitative organization of search patterns; and (d) describing the dynamics of their emergence in the course of task practice.

Method

Subjects

The subjects were 4 capuchin monkeys (*Cebus apella*): a captive-born female, 13 years old (Subject BR); a wild-born male, approximately 6 years old (Subject NA); a captive-born male, 5 years old (Subject PA); and a wild-born female, approximately 6 years old (Subject VI). All the monkeys were socially housed at the Institute of Psychology of the Consiglio Nazionale delle Ricerche in Rome, Italy. Each subject was separated from the group only for the purpose of 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 groupmates. All the subjects had participated in a previous experiment featuring a search task that used the same apparatus (De Lillo et al., 1997).

Apparatus

The experiment was conducted in a square cage (3.0 m wide \times 2.5 m high). Three walls of the cage were made of concrete, and the floor was made of concrete and metal bars. The fourth wall and the top of the cage were made of wire mesh. In each of the three concrete walls, a guillotine door was installed. On the three concrete walls, a perch of the same length of the wall allowed the monkey to easily reach the ceiling of the cage. The cage was illuminated by a neon lamp from above the top of the cage. Therefore, the monkeys had many landmarks because of the asymmetrical features of the cage. Nine opaque plastic containers were suspended by a metal chain approximately 5 cm long that was hooked to the top of the cage. The containers were identical in shape (cylindrical), size (a diameter of 3.0 cm; a depth of 2.5 cm),

and color (gray). A reward (half a peanut) was hidden in each of the nine containers. This arrangement allowed the monkeys to easily recover the reward, but they could not see the reward from any point in 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 a guillotine door. The waiting cage where the subject was kept before each trial was selected pseudorandomly to prevent the subject from entering the testing cage from the same side on more than two consecutive trials. After the baiting procedure was completed, the guillotine door was lifted, and the subject entered the testing cage and was permitted to search the containers to retrieve the bait. The experimenter allowed the subject to exit from the experimental enclosure by reopening the guillotine door, either when it had visited all the containers (exhaustive search) or when 15 min had elapsed, whichever occurred first. There was an interval of 3 min between successive trials, during which the containers were rebaited.

The experimental design featured six conditions. Each condition comprised 60 trials. Monkeys were tested 5 days a week. Each daily session comprised 12 trials. For each condition, the spatial arrangement of the set of containers was manipulated as follows:

Condition A. Condition A was a baseline condition. The spatial arrangement of the containers was a 3×3 matrix with a distance of 60 cm between two adjacent containers. (see Figure 1a).

Condition B. This condition featured an X-shaped configuration of containers. (The relative distance of adjacent containers is reported in Figure 1b.)

Condition C. This condition featured a linear arrangement of containers (see Figure 1c). The distance between adjacent containers was 40 cm. The orientation of the line conformed to the diagonals of the square ceiling of the cage. The 12 trials of each daily session were divided into two blocks of 6 trials, each block featuring the orientation of the line according to one of the diagonals of the ceiling of the cage. The order of presentation of the blocks was randomly chosen on daily basis.

Condition D. In this condition, the configuration of containers presented in Condition B (see Figure 1b) was reestablished to evaluate the possible transfer effects the monkeys might have experienced because of their exposure to the linear arrangement of containers in Condition C.

Condition E. This condition featured a circular arrangement of containers. The center overlapped with the center of the cage. The diameter of the circular configuration was 240 cm, and the distance between adjacent containers was 60 cm (see Figure 1d).

Condition F. The spatial arrangement featured in the baseline condition (Condition A, Figure 1a) was reestablished to see whether effects attributable to the experimental conditions (Conditions B to E) could instead be merely due to 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 checksheet.

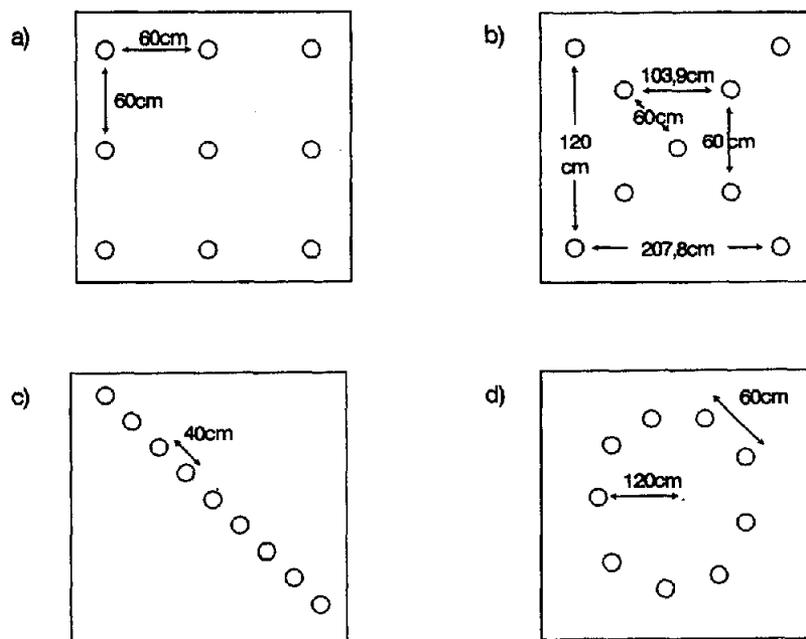


Figure 1. Scheme of the spatial configurations of the search space used in the different conditions of the experiment: (a) baseline and control conditions, featuring an arrangement of containers according to a 3×3 matrix; (b) condition featuring an X-shaped configuration of containers; (c) condition featuring a linear arrangement of containers; and (d) condition featuring a circular arrangement of containers.

Results

Search Efficiency

The subjects spontaneously performed exhaustive searches in all the trials presented for each condition. An analysis conducted on the number of correct choices within the first nine (a measure commonly adopted in radial-maze-based studies) that were observed for each subject in each of the conditions revealed values ranging from 7.08 (Subject PA, Condition A) to 8.82 (Subject NA, Condition E). A series of *z* tests revealed that all the values were significantly ($p < .001$) above the expected 5.87 chance level (Spetch & Wilkie, 1980). Therefore, all our subjects proved to be proficient searchers in a variety of different spatial configurations. After we had assessed this ability, we evaluated the relative efficiency of the monkeys' searches in the different conditions presented. We measured search efficiency in terms of the number of moves (visits to containers) the monkeys performed before they completed the exhaustive search of the set of containers. We analyzed this measurement by means of a mixed-design analysis of variance (ANOVA), Subject (4) \times Condition (6) \times Blocks of Trials (5).

A significant difference emerged between conditions, $F(5, 220) = 56.45, p < .001$. As shown in Figure 2, there was a dramatic decrease in the average number of moves in the conditions featuring a linear and a circular arrangement of loci. Post hoc comparisons showed that whereas the number of moves per trial observed in the conditions featuring a linear and a circular arrangement of loci did not differ between each other, they both differed from the number of moves per trial observed in all the other conditions at a probability level of $p < .001$. The two conditions featuring an X-shaped configuration of loci (Conditions B and D) both differed from Condition A, which featured a matrix of loci (B vs. A, $p < .01$; D vs. A, $p < .001$). Even though Condition

F presented a configuration identical to that in Condition A, a significant difference ($p < .001$) emerged in the average number of moves per trial observed in the two conditions. This result points toward an effect of task practice quite independent from the effect produced by the shape of the configuration.

Overall, these results show that the linear and the circular spatial structure of the search space produced the most dramatic results on the search economy of the monkeys. Given the significant increase (shown by the post hoc comparisons mentioned above, $p < .001$) in the number of moves per trial in Condition F compared with both Conditions C and E, this effect has to be attributed to the shape of the configuration and not merely to task practice.

The analysis of the main effects also demonstrated a significant difference between subjects, $F(3, 44) = 22.8, p < .001$, and a significant interaction of Subjects \times Condition, $F(15, 220) = 3.27, p < .001$. As shown in Figure 2, the Subject \times Condition interaction does not lessen the importance of the condition's main effect because the pattern of results is the same for all the subjects. Moreover, the interaction is accounted for by the variance of the results obtained in particular conditions only, namely Conditions A, B, D, and F, whereas a lower variance can be observed in the data concerning Conditions C and E. These latter conditions, therefore, induced a more uniform performance among the subjects.

From planned comparisons between conditions performed for each of the subjects, neither sex- or age-related groupings could be observed.

As for the group analysis, no significant difference between Conditions C and E emerged for any of the subjects. For all the subjects, Condition C produced different results from all the other conditions at a significance level of at least $p < .01$, with the exception of the results for Subject NA,

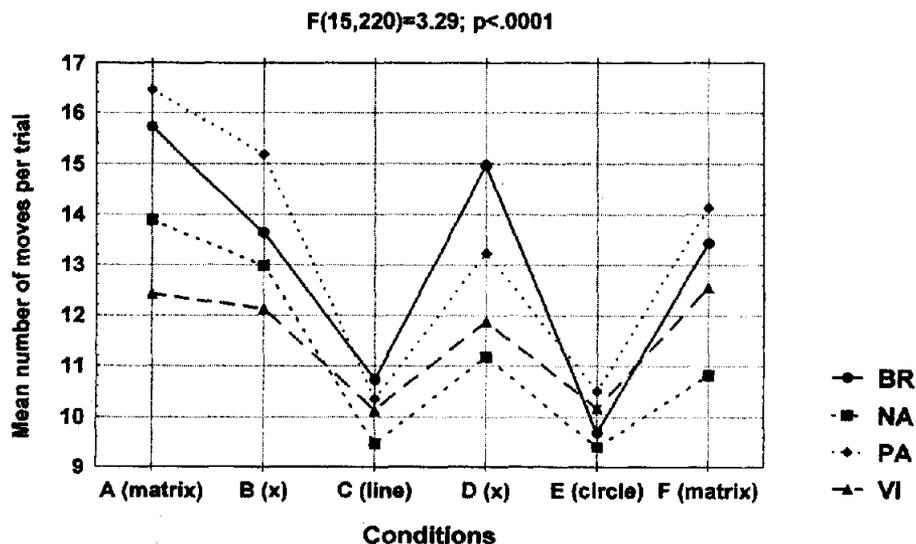


Figure 2. Average number of moves in which exhaustive searches were completed by each subject (BR, NA, PA, and VI) in the different conditions.

which showed a level of significance of $p < .05$ in the comparison between Conditions C and F and Conditions E and F.

Thus, results obtained by analyzing the performance of individual subjects strongly support evidence from the analysis of group results: A linear and a circular organization of the search space produced the most dramatic results on the search economy of the monkeys.

Analysis of the Microdevelopment of Search Efficiency

So far, we have presented data showing that the observed differences between conditions cannot be explained on the basis of an effect of transfer of learning among conditions. In this section, we will focus on the assessment of changes produced in search efficiency within each of the conditions.

An analysis of the trend in the number of moves performed on the five different blocks into which each of the conditions was divided showed that in none of the conditions did the group of subjects practicing the task reduce the number of moves according to a linear component.

We obtained the same results when we individually analyzed each of the subjects. The only exceptions were Subjects BR and PA; they showed a slight reduction in the number of moves per trial in Conditions B, $F(1, 11) = 5.16$, $p < .05$, and C, $F(1, 11) = 6.67$, $p < .05$, respectively. Apart from these exceptions, each condition produced a steady-state performance from the outset.

We conducted a further analysis to evaluate whether proactive interference (Roberts & Dale, 1981) influenced the results. Specifically, we tested the hypothesis that the average number of moves performed by the subjects in the first four trials of each daily testing session was lower than the average number of moves in the last four trials of each daily testing session. An ANOVA with Subject \times Condition \times Groups of Trials (first four vs. last four) revealed no effect of group of trials, and the only significant interaction involving the group factor was Subject \times Group, $F(3, 76) = 2.8$, $p < .05$. Post hoc analyses revealed that the significant interaction was due to Subject NA's improving performance from the first group of trials to the second (12 vs. 11 moves respectively, LSD test, $p < .04$), which contrasted with the unvarying performance of the other subjects.

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 (as opposed to a random selection of one site after the other without any principle of spatial organization) in the absence of explicit training. The organization of searching is expressed in the pattern of transitions from one site to another during search. Therefore, we used the chi-square test (1 degree of freedom) to analyze the transition frequency matrices obtained from the observed moves of the subjects (see De Lillo et al., 1997, or Van Hoof, 1982, for a description of the method and the formula). We

used the same method to check whether subjects had a tendency to start and end the search in particular positions and to compare the number of transitions performed on adjacent containers with those expected by chance (for more details, see De Lillo et al., 1997).

The patterns of transitions were significantly different from those expected by a random walk within the search space ($p < .05$ for each of the subjects in each of the conditions). Moreover, each of the subjects had preferred starting points ($p < .05$ for each of the subjects in each of the conditions) and a tendency to move to adjacent locations more than expected by chance ($p < .001$ for each of the subjects in each of the conditions).

Thus, the monkeys did not follow random trajectories while searching. Moreover, individual differences were observed in the pattern of transitions spontaneously selected by each of the subjects. These patterns and the preferred starting (S) and ending (E) locations that resulted from the analysis are reported in Figure 3.

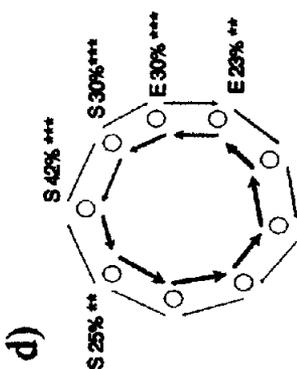
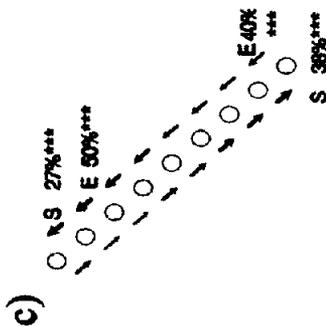
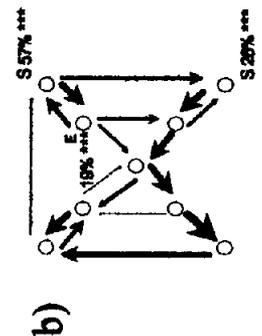
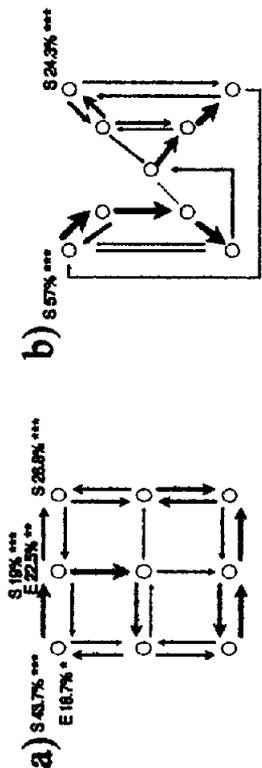
Analysis of the Microdevelopment of Search Organization

The analysis of the transitions reported in the previous section shows that the search patterns of the monkeys were not random on the whole. However, this analysis took into consideration the overall set of data without partitioning it into different blocks of trials. It is, however, possible that the subjects gradually developed very principled search patterns in the course of task practice. The aim of the analysis reported in this section is to evaluate the microdevelopment of search organization (Karmiloff-Smith, 1992) across blocks of trials of principled search trajectories in conditions where high levels of search efficiency were observed. In other words, this analysis is aimed at evaluating possible dynamic changes in the search patterns as a function of task practice in Conditions C and E.

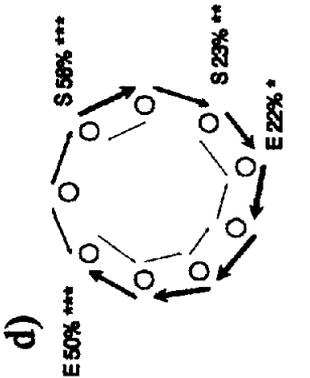
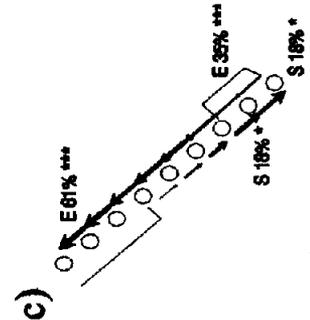
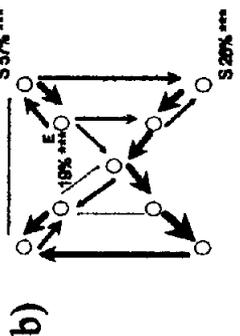
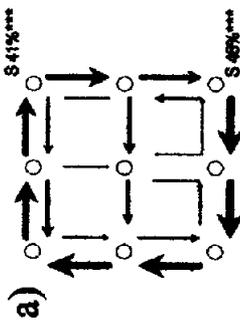
Condition C. As we demonstrated above in the section concerning the analysis of search efficiency development, the performance of the subjects (in terms of number of moves) was constant across the blocks; the only exception was Subject PA, whose performance improved in this condition. Nevertheless, a trend was present in the number of occasions in which an end-to-end search was observed in each block of trials, $F(1, 3) = 12.87$, $p < .05$. The percentage of end-to-end searches across blocks of trials is reported in Figure 4 (left Y axis). This trend strongly contrasts with the nearly flat performance of the monkeys in terms of number of moves performed to complete search (also shown in Figure 4, right Y axis). In fact, a Spearman r test for correlation conducted on the average number of moves across blocks of trials and the percentage of end-to-end searches bears no statistical significance ($r = -.04$, $n = 20$, *ns*). It seems therefore that in the presence of a steady-state performance the subjects were further regulating their behavior. This regulation was expressed mainly in the search pattern.

Figure 5 shows the pattern of transitions as observed in the first (a) and the last (b) block of trials presented in Condition C. In the first block of trials, the subjects had the

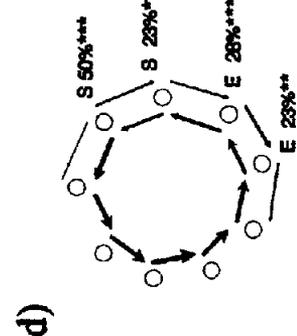
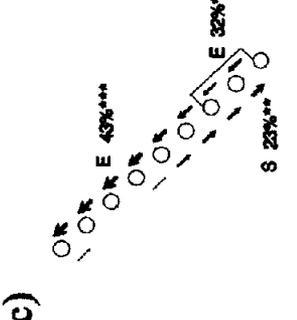
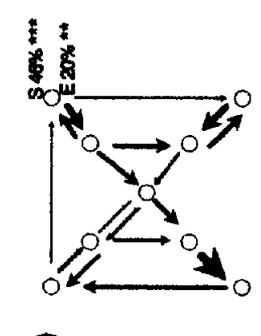
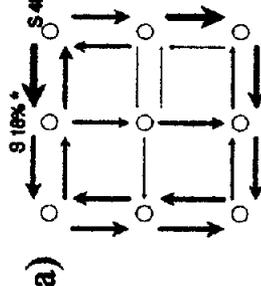
NA



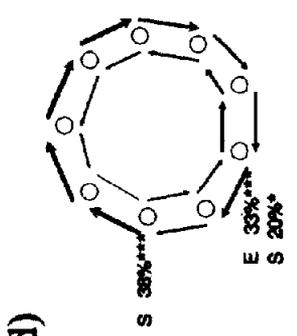
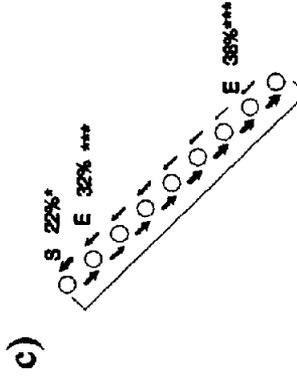
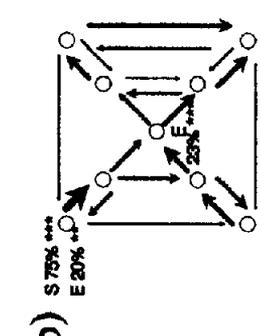
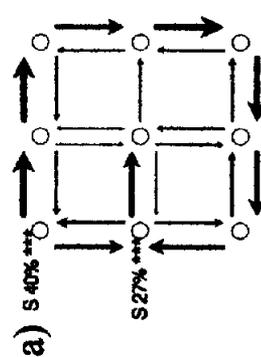
BR



PA



VI



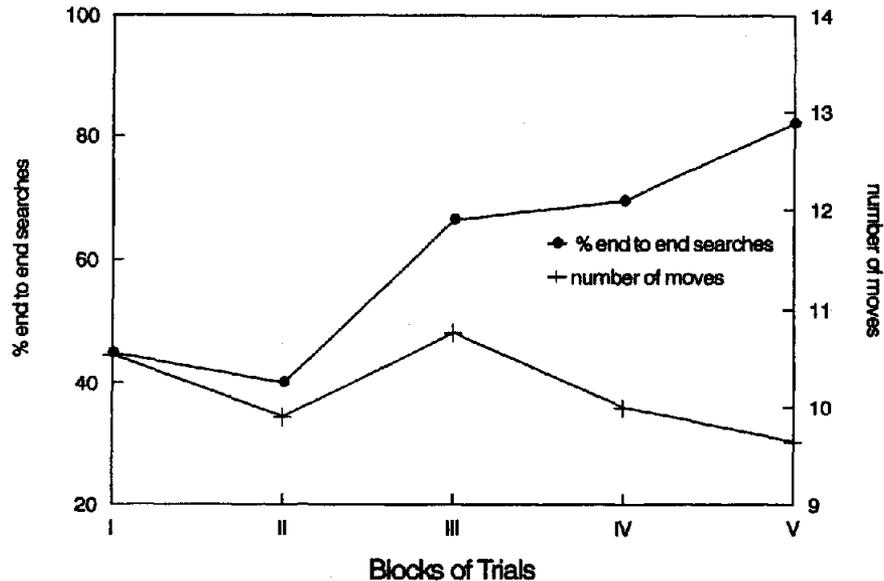


Figure 4. Right Y axis = percentage of searches that started from one extreme of the line and ended on the opposite one (end-to-end searches) in successive presentations of blocks of 12 trials each. Each block corresponds to a daily testing session. Left Y axis = average number of moves performed by the 4 subjects in successive presentations of blocks of 12 trials each.

tendency to start searching at a container located between the two end points of the line. The subjects then moved onto adjacent containers in one direction until they reached an end point. Finally, the subjects changed their direction of travel after having skipped the containers already visited. In contrast, in the last block of trials, end-to-end searches became the most frequent travel trajectories through the search space. It has to be stressed that both patterns of search led to a high level of performance in terms of number of moves per search.

Condition E. Whereas a linear arrangement of loci implicitly suggests a starting and an ending point (the two extreme points of the line), a circular arrangement, such as that in Condition E, does not. If a subject wanted to use the configuration as a notational system and sustain optimal searches, it could start from one of the containers and move to adjacent ones, always following the same direction of travel (either clockwise or counterclockwise). The problem for a subject using this strategy is to stop just before repeating a visit to the starting point and thus to avoid loops.

To do this, it would be useful for the subject to always start from the same location, store it in long-term memory, and stop just before repeating it in each trial. As we have already demonstrated, our subjects showed, in Condition E, a strong tendency to select preferred starting points and to move to adjacent locations, always following the same direction of travel, without inverting it within each trial.

To check whether the subjects consolidated this strategy in the course of task practice, a trend analysis was conducted on the frequency of trials characterized by a starting point that corresponded to one of the preferred starting points for that subject and a circular pattern of travel without inversion of direction in each block of trials. The trend analysis only approached statistical significance, $F(1, 3) = 7.39, p = .072$.

Analysis of Redundant Moves After Search Completion

The dynamic changes in search organization described above also led to a decline in the number of visits by the

Figure 3 (opposite). Transitions performed between successive moves within the search space by each subject (BR, NA, PA, and VI); (a) conditions featuring a matrix; (b) conditions featuring a cross; (c) condition featuring a line; and (d) condition featuring a circle. For each subject, the transitions performed when searching different configurations are reported. Data obtained from conditions featuring pairs of identical configurations (Pair A and F and Pair B and D) have been collapsed for the analysis. Only statistically significant transitions (see the text for more details on the data analysis) are reported as arrows. The thickness of the arrows is proportional to the observed frequency of the transition. Only the starting and ending points selected above chance level (see the text for more details on the data analysis) are reported. For each starting and ending point, the percentage of trials in which that particular location was observed as a starting or ending point is reported. S = preferred starting positions; E = preferred ending positions. * $p < .05$; ** $p < .01$; *** $p < .001$.

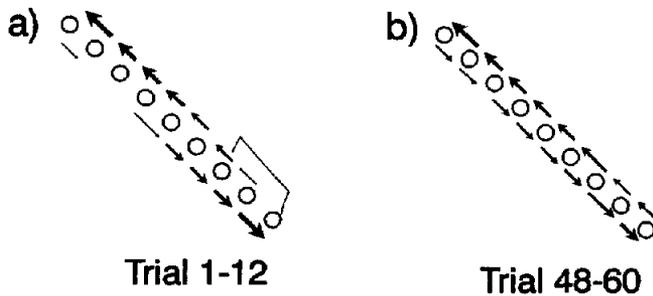


Figure 5. Microdevelopment of search organization in Condition C. Transitions performed between successive moves within the search space by all the subjects ($N = 4$) in the first (a) and the last (b) block of the 60 trials for this condition. Only statistically significant transitions are reported as arrows. The thickness of the arrows is proportional to the observed frequency of the transition.

subjects to empty containers after having exhausted the set. In fact, trend analyses conducted on the frequency of moves observed after search completion revealed a strong linear component in both Conditions C, $F(1, 44) = 12.35, p < .01$, and E, $F(1, 44) = 10.33, p < .01$, which accompanied the increase in search organization, as described in the previous section. The average number of moves postcompletion was significantly different, $F(1, 44) = 24.53, p < .001$, in Conditions C (0.98 ± 1.86) and E (1.83 ± 2.01). It is therefore evident that the average number of postcompletion moves tended to 0 in Condition C and 1 in Condition E, suggesting that whereas the linear array provides unequivocal information about the completion of a search, the circular configuration induces the use of a strategy consisting of one postcompletion move that acts as a stopping signal for the subjects.

Discussion

Our study was aimed at the evaluation of the ability of capuchin monkeys to efficiently search a set of containers arranged according to a variety of spatial structures. Using an apparatus that allowed the flexible manipulation of the spatial structure of the search space and where subjects could not rely on external cues inevitably left at each visit, we were able to demonstrate that capuchins are proficient searchers of structures as different as a matrix, a cross, a line, and a circle. In fact, the proficiency of the monkeys was demonstrated by their ability to always perform exhaustive searches within a set of nine containers.

The spatial structure of the configuration seemed to produce a dramatic effect on the search economy of the monkeys. In fact, we observed a nearly optimal performance in search spaces, such as a line and a circle, which can be used (by means of basic strategies) as notational systems.

In a previous study, De Lillo et al. (1997) had already shown that capuchin monkeys show very principled search patterns in configurations that present a set of nine containers organized in spatial clusters. The search patterns observed in the series of transitions performed by the monkeys consisted of always exhausting a cluster before moving to a

new one. Such a search pattern allows, by analogy to psychological chunking (Dallal & Meck, 1990; Miller, 1956; Terrace, 1987), the reduction of the memory load from the total number of loci to be explored to the number of clusters into which the search space is divided.

Our results show that capuchin monkeys are able to flexibly organize their search behavior in configurations, such as a line and a circle, that have strong spatial constraints but are not isomorphic to a patchy foraging space. By doing so, they produce very economical searches.

A further finding of our study is the result obtained from the analysis of the microdevelopment of search trajectories in the condition featuring a linear arrangement of containers. There, we observed that subjects progressively produced a change in their behavior according to the shape of the configuration presented. Because the performance (in terms of number of moves per trial) remained constant across trials, we can rule out the hypothesis that monkeys were regulating their behavior using the amount of redundant moves as a source of feedback. What sort of feedback information were monkeys using to learn to explore the configuration starting from one extreme and ending at the opposite one? We can conceive of only two possible explanations. The first is that monkeys were simply trying to minimize the traveling distance. An end-to-end search is the shortest trajectory through a linear search space. Thus, any deviation from such a principled search pattern would add costs (either in terms of energy or time spent searching) to the search process. If this explanation applies, monkeys might have been monitoring the costs associated with longer trajectories and reduced them in the course of task practice, thus gradually producing a high percentage of end-to-end search patterns. This hypothesis finds support in the affluent amount of data coming from other studies that, using search tasks, showed that monkeys (McDonald & Wilkie, 1990), apes (Menzel, 1973), and indeed nonprimate species minimize traveling distance.

On the other hand, we can speculate about the presence of cognitive costs (De Lillo, 1996; Terrace & McGonigle, 1994) associated with the search process. These costs could be related to the amount of information the subjects have to memorize to avoid redundant moves. From that perspective, a subject using an end-to-end search pattern within a linear configuration of loci and always moving to adjacent loci would not need to memorize the locations already visited. The particular point of the trajectory the subject is in, at any given moment, would tell it unambiguously the loci already explored and those which remain to be explored (De Lillo, 1996). This would be a very robust strategy because the trajectory itself could act as a notational system (Karmiloff-Smith, 1992) that would allow a maximum search efficiency, avoiding the overload of the memory system even when the number of loci to explore is increased along the same array.

As a comparative note, it is interesting to mention that pigeons confronted with the task of performing a search within different configurations of keys on a panel perform better when the configuration is a matrix than when they are presented with a linear array (Zentall, Steirn, & Jackson-Smith, 1990). Of course, the apparatus and procedures

adopted in the pigeon study were quite different from those used here. However, the isomorphism of the configurations presented here and those in Zentall et al.'s study make it possible that while monkeys can benefit from search spaces that have strong structural constraints, pigeons might not be able to do so.

Similar evidence supporting a difference between monkeys' and birds' search modes comes from a study by Spetch and Edwards (1986) involving a task similar to ours. There, pigeons faced simulated foraging environments featuring a circular and a linear arrangement of food sites. Some of the birds had a strong tendency to search the circular space (analogous to a radial maze) by preferentially selecting adjacent locations. However, this tendency was often coupled with frequent inversions of the direction of travel. Although these inversions did not lead to incorrect choices by the pigeons, their behavior contrasts with the search mode we observed in our subjects. In fact, for the monkeys in this experiment, the selection of adjacent food sites was always accompanied by a directional principle that prevented the inversion of the direction of travel. It can be noted that only this latter strategy would allow the use of the configuration as a notational system.

Thus, monkeys seem to use a more complex strategy (or at least to integrate more substrategies) than pigeons when faced with a circular arrangement of loci. However, the most striking difference between our results and those of Spetch and Edwards (1986) emerges when the search behavior of pigeons on linear arrangements of loci is examined. When pigeons were faced with a linear arrangement of loci (two parallel rows), none of the subjects followed a search pattern that consisted of moving along one of the lines. Spetch and Edwards could not detect any principled response pattern in the behavior of the birds and therefore claimed that the high level of performance observed in the pigeons had to be accounted for by good spatial memory competence.

Of course, further research is necessary to fully appreciate the relative role played by cost-reduction functions based on different currencies such as traveling distance and memory load. Likewise, data must be collected on other species to evaluate whether the currency for regulation is the same in primate and nonprimate species. However, we believe that tasks such as those presented here tap into dimensions that might prove relevant for the differentiation of organisms on the basis of their level of cognitive complexity and, as such, these tasks are invaluable for the comparative psychologist.

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