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Explorations of three modes of spatial cognition in the monkey

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This paper is organized around three major areas: (i) First, we review a series of our own studies on spatial cognition of monkeys that had received hippocampal resections or fornix transections in infancy and that appeared to have recovered from their initial deficit on a left-right spatial discrimination task. The results from our long-term follow up study of these monkeys showed that, in spite of their improved performance on left-right discrimination, and their facilitated spatial learning in the presence of allocentric landmarks, monkeys with hippocampal damage showed a profound impairment on the trial-unique position recognition task and on the recognition span task. (ii) A second major section is dedicated to present an overview of some experimental field studies on primate spatial learning and memory in ecological settings. Even though this section does not reflect the authors direct experience, we considered it of importance to provide the reader with findings obtained from this type of studies, which may serve as an important source of evidence for hypothesis development; and (iii) Finally, this paper includes a partial review of neuropsychological and neurophysiological studies on some of the parietal, temporal or frontal brain areas which have been implicated as subserving one or another mode of spatial cognition. Thus, rather than attempting to provide an exhaustive review, we have oriented this paper towards stimulating and capturing the interest of the reader with a sample of the wide array of approaches that can contribute to the study of spatial cognition in nonhuman primates.

The search for an experimental model of hippocampal functions in the monkey: The early studies

It has been a widely accepted view among neuropsychologists that the integrity of medial temporal lobe structures, and particularly that of the hippocampus, is essential for normal memory and spatial function in humans. This notion emerged from reports that described patients who presented

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selective and severe anterograde amnesia, following temporal lobe resections intended to alleviate uncontrollable epileptic seizures, or profound psychotic disorders (Scoville, 1954; Scoville and Milner, 1957; Penfield and Milner, 1958). In most operations performed with this purpose, surgical removals were restricted to the amygdaloid complex and the surrounding pyriform cortex; while in some other cases, the removed tissue also included the anterior portion of the hippocampus. However, in two of Scoville's patients, and in an attempt to obtain greater therapeutic effects, the excisions were extended caudally, to include the main body of the hippocampus. It was these two patients with more radical bilateral resections who emerged from postoperative care with dramatic immediate memory impairments, and spatial disorientation. It was on the basis of this unexpected finding, not found in approximately twenty other patients, whose removals did not include the hippocampus (i.e., only circumscribed to the amygdala) that the hippocampus began to be considered as a key brain structure for normal memory function.

Stemming from these initial clinical findings, and with the purpose of gaining a better understanding of the neurological mechanisms underlying memory and spatial function, there soon began several investigations on the effects of hippocampal lesions in experimental animals. The first studies were focussed on the effects of medial temporal lesions, virtually copied from Scoville's (1954) original surgery. In fact it was Scoville himself who performed some of the ablations in monkeys (Correll and Scoville 1965; 1970). In general, the first investigations were not successful in demonstrating comparable deficits to the amnesia seen in patients.

One of the most systematic experimental attempts to clarify the behavioral functions of the hippocampus has been developed by Helen Mahut and her co-workers. With the purpose of defining the behavioral role of the hippocampus and of obtaining a more precise verification of the locus of damage, they studied the postoperative effects of hippocampal damage in nonhuman primates, using two different experimental strategies: The first one was to vary the site of lesion; thus, for example, in some groups of young adult rhesus macaques, the hippocampus was excised; in others, they left the hippocampus intact, but a major afferent and efferent pathway of the hippocampus was interrupted by sectioning the fornix, or by ablating the entorhinal and inferotemporal cortex. In spite of its systematic precision, this behavioral exploration of the hippocampus uncovered a pattern of deficits, which did not resemble in quantity, or quality, the clinical phenomena of amnesia and spatial disorientation that was observed in patients with medial temporal damage.

The second strategy consisted of varying the age at which lesions were performed, keeping in mind two specific goals: One was to uncover whether the impairments observed in adult monkeys with hippocampal damaged reflected impairment in one, or more than one, altered functions; and the other, was to contribute data towards the clarification of the interesting conflicting evidence on the consequences of early versus late brain damage (Schenider, 1979).

As part of the latter of these two approaches, earlier studies in Mahut's laboratory, showed that ablations of the hippocampus sustained by infant monkeys, at two months of age, had differential effects on performance on two tasks in which adult monkeys with equivalent damage are typically impaired: While the performance of operated infants was spared on retention and re-learning of two-object discrimination 1-hr, or 24-hrs, following acquisition, it was unspared on left-right spatial discrimination reversal learning (Mahut and Zola, 1976; 1977; Mahut and Moss, 1985). A Subsequent follow-up investigation, using nonspatial learning and memory tasks, provided another example of spared learning capacity which co-existed with a sizable impairment in recognition and associative memory capacities. The findings, which led to the demonstration of this behavioral dissociation, were presented elsewhere (Mahut and Moss, 1985).

The studies reviewed in the present report were part of a follow-up investigation of the initial impairment, and later recovery, of the performance of those same operated infant monkeys on the spatial reversal task (Rehbein, 1985a; 1985b; 1991).

Egocentric, left-right spatial discrimination learning tasks

Spatial reversal task. In the spatial reversal task, monkeys must learn to find the bait first under the left of two identical plaques. After a learning criterion of 18 correct responses in 20 trials is met, the bait is placed under the opposite plaque (reversal) until learning criterion is met again. Infant monkeys with either hippocampal or fornix damage, were severely impaired on five such reversals, administered in succession, and the severity of the impairment resembled that seen after equivalent damage in adults (Mahut and Zola, 1976; 1977). Normal and operated infant monkeys in these studies were tested with the spatial reversal task on three occasions. The first, postoperatively, at approximately 3 months of age, then twice more, at one year intervals. On the last re-test, two and a half years after surgery, operated groups no longer differed significantly from the normal, control group, though individual operated monkeys were still impaired (Mahut and Moss, 1985).

On the basis of these early findings, however, it was unclear whether the improved performance of operated monkeys was due to repeated practice with the spatial reversal task, or it represented a more general recovery of spatial learning capacity. The series of studies we review here was undertaken to clarify this question by administering previously unencountered spatial tasks to the same monkeys from the studies by Mahut and Zola (1976; 1977). More specifically, we are going to address the results obtained from testing the following groups of subjects: Seven monkeys with early bilateral hippocampal resections (group H); four monkeys with early bilateral sections of the fornix (group BF) and five unoperated control monkeys (group N). There was an additional group of monkeys, which had sustained unilateral

sections of the fornix; however, for the sake of brevity, is not included in the present review.

Delayed alternation task. In a first experiment, normal and operated monkeys were tested with the Delayed Alternation task, an unfamiliar left-right discrimination task on which, like on spatial reversals, adult monkeys with hippocampal or fornix damage are known to fail (Mahut, 1971; 1972).

In this task, as in all other tasks we are going to describe in this section of our review, testing took place in a modified Wisconsin General Testing Apparatus. The experimenter sat behind a one-way screen facing the testing tray, which, between trials, was concealed from the monkey by an opaque door. Raisins, pieces of apple, or other highly preferred foods were used as bait. On the delayed alternation task, the tray contained two food wells 35 cm apart, center-to-center, and monkeys were required to choose, alternately, the left or the right food-well to obtain reward. A preliminary unscored trial preceded each daily session during which both wells were baited, covered with two identical black plaques, and a free choice was allowed. On the first scored trial, the bait was placed in the well that had not been chosen on the preliminary trial. A non-correction method was used throughout the task with inter-trial intervals of approximately 5 seconds. Thirty trials a day were given until a learning criterion of at least 90 correct responses in the last 100 trials, was met, or to a maximum of 960 trials. A summary of the results is presented in Table 1.

Table 1. Learning scores obtained by normal and operated monkeys on the spatial (left-right) delayed alternation task.

Groups	<u>n</u>	Mean trials	Mean errors
Normal control	5	512	147
Bilateral fornix	4	462	140
Hippocampal	7	685	179

No significant group differences in learning scores were found, though several operated monkeys took longer to learn than any of the normal monkeys. This experiment, intended to assess the effects of practice with the spatial reversal task on performance on an unfamiliar spatial task, provided another example of unimpaired group performance. However, as with the third administration of the spatial reversal task, two and a half years after surgery, at least half the monkeys in group H were still impaired on left-right discrimination learning. Thus, the initial question about whether recovery on spatial reversals was task-specific or rather represented a more general recovery of spatial function, could not be answered adequately (Rehbein, 1985; 1991).

Allocentric, landmark based spatial discrimination tasks

Landmark discrimination task. In an additional attempt to answer this question, a different approach was to see whether the spatial learning of operated monkeys would improve if the location of the positive one of two identical objects could be discerned relative to an external referent ('allocentric' cue), rather than relative to the monkey's own body. In the next two experiments, monkeys were tested on two new spatial tasks that differed from the delayed alternation task in that they could be solved by the use of an alternative spatial strategy. With the delayed alternation task monkeys must learn to discern the left from the right food well in reference to their own body (egocentric cues). Therefore, in a second experiment, the addition of a distinct object (landmark) on the testing board was expected to serve as an external referent (allocentric cue), and that monkeys would find it easier to guide their responses relative to it, than they would do relative to their body. If this were the case, no impairment was expected. This task required the monkeys to shift their responses from the left to the right one of two identical plaques, presumably, with no additional cues available other than the orientation of their previous response relative to their own body ('egocentric' cues). In an earlier study, Pohl had demonstrated the existence of such two reference systems in the spatial learning of monkeys (Pohl, 1973). He found that, while dorsolateral prefrontal cortical damage impaired performance on a left-right discrimination task, it did not affect performance on a landmark discrimination task. Conversely, posterior parietal damage impaired performance on a landmark discrimination task but left that on left-right discrimination intact.

Thus, in a second experiment, as in Pohl's (1973) study, a three-dimensional object (landmark) was added onto the testing tray. The landmark was expected to guide the monkeys' responses without the need for them to depend, exclusively, on an egocentric frame of reference. However, since in Pohl's (1973) study, the landmark was always in physical contact with one of two identical plaques, it is possible that monkeys viewed the display as a complex visual configuration, which could have masked the spatial nature of the task. In order to avoid this possible source of confounding, we used a testing tray with 18 food wells and moved the location of two identical objects and the landmark relative to one another from one trial to the next. The object to the right (or the left) of the landmark was to be the positive one, regardless of the visual configuration of the three elements on any given trial. An illustration of the testing tray is presented in Figure 1. If the spatial performance deficit of monkeys with hippocampal or fornix damage was linked with an impairment to deal with an egocentric frame of reference, no impairment was expected on the landmark discrimination task. Additionally, in order to uncover whether the visual landmark was in fact responsible for the lack of impairment, we decided to assess the effect of removing the landmark on monkeys' performance during an additional testing session, after learning criterion was reached.

All monkeys learned the landmark task rapidly, within 2 to 13 sessions, and no significant group differences in performance were found. However, monkeys in group H obtained significantly higher error scores on transfer

trials, during the additional session without the landmark. These data are summarized in Table 2.

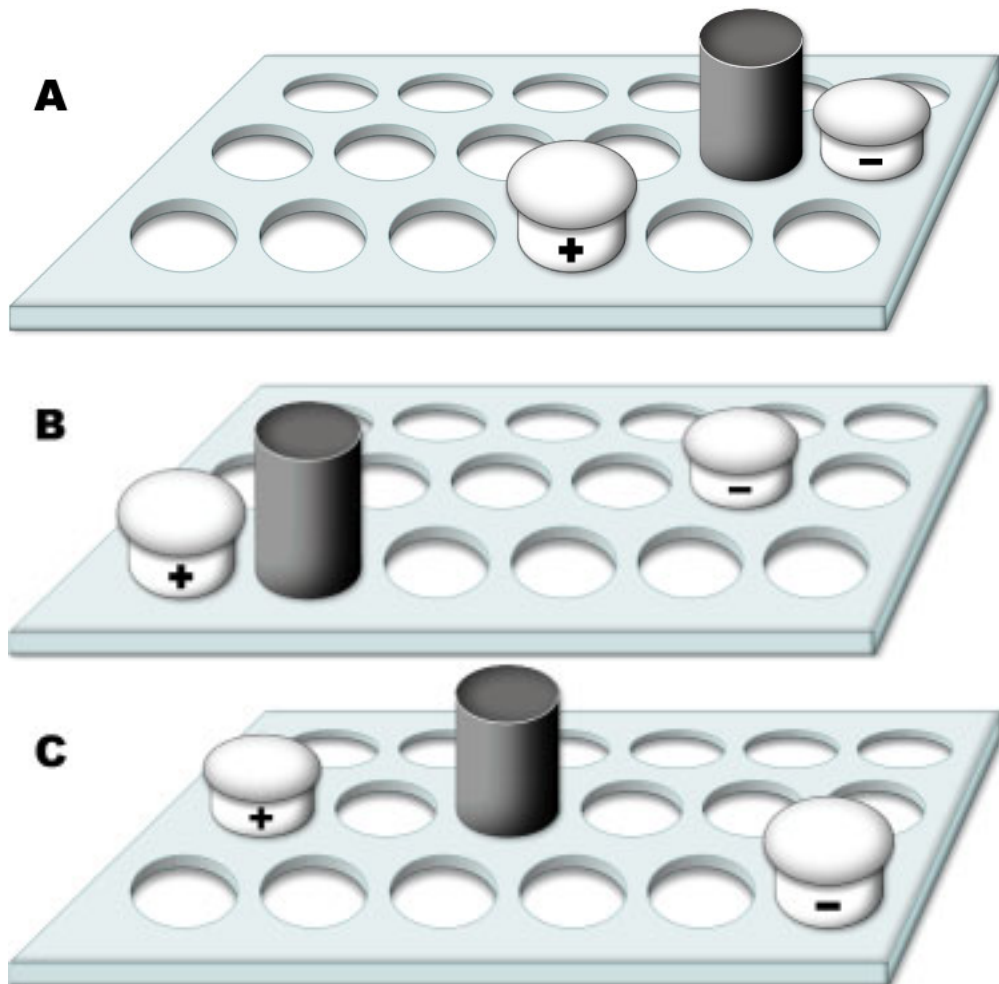


Figure 1. Illustration of the procedure used in the landmark discrimination task, with examples of three trials. A: The landmark and the two objects to one side of the center of the tray. B: The landmark, together with one of the objects, on one side of the center of the tray and the other object on the opposite side. C: All three objects dispersed across the tray. “+”: Denotes presence of food reward. “-”: Denotes absence of food reward.

The landmark was expected to help monkeys in the hippocampal group to perform as well as did those in the normal group by, presumably allowing them to respond under visual guidance in reference to an allocentric cue. However, on hindsight we realized that, while it was true that the positive object was always to the right (or the left) of the landmark as intended, it was also, unfortunately, always to the left (or the right) of the monkey. Therefore, the task shared an important 'egocentric' component with the spatial reversal and delayed alternation tasks. However, that the landmark did play a role was indicated by the deterioration in the performance of monkeys in the hippocampal group in its absence, but this role was not strong enough to readily allow monkeys to develop a guidance strategy in allocentric space.

Table 2. Learning scores obtained by normal and operated monkeys on the spatial (left-right) discrimination task with landmark.

Groups	n	Mean trials	Mean errors	Errors on Ransfer sess.
Normal control	5	96	26	0.6
Bilateral fornix	4	127	32	1.7
Hippocampal	7	158	36	3,2*

Note. (*) In spite that monkeys in group H learned as readily as did those in group N, they made significantly more errors during the transfer session, without the landmark, $p < .05$.

Asymmetric landmark discrimination task. The next step, therefore, was to design a task, which would provide a more effective means of guiding the monkey allocentric spatial learning. Unlike the cylindrical landmark used in the preceding experiment, which had no distinct sides but those extrapolated by the observer, we decided to provide a new landmark that was to be asymmetric in shape, so that it would have its own orientation in space. This condition was achieved by using a landmark in the shape of an arrow, mounted on a rotating tray, so that no matter how the visual array was rotated, the relationship between the head and body of the arrow remained unchanged. This time the landmark would have its own changing orientation, independent of the point of view of the observer, and one of two identical objects would truly be to *its* right (or *its* left), rather than to the right (or left) of the animal's body (See Figure 2).

Under these corrected conditions, the elevated scores previously still shown by some of the monkeys with ablation of the hippocampus should no longer be found.

In fact, this time monkeys in groups H and BF were not only unimpaired, but made significantly fewer errors than did those in group N. These results showed that the two groups of operated monkeys were

effectively helped by the presence of an asymmetric visual landmark in allocentric space. A summary of these data is presented in Table 3.

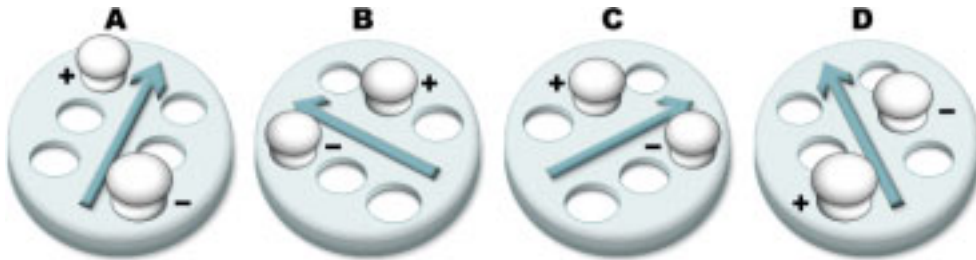


Figure 2. Illustration of the procedure used in the spatial discrimination task with asymmetric landmark with examples of four trials. Letters A, B, C and D: Denote landmark orientations set at 1, 10, 2 and 11 o'clock, respectively. "+": Denotes presence of food reward. "-": Denotes absence of food reward.

An analysis of error patterns showed that the observed facilitation in performance by operated monkeys could be accounted for by at least two factors: (i) Normal monkeys spent on the average 4 days approaching the task with a readily available, but ineffective, egocentric, near-far spatial hypothesis; (ii) The great majority of monkeys in the two experimental groups did not adopt a systematic egocentric near-far, or left-right, spatial strategy, but were able to develop a guidance strategy, presumably based on the cues provided by the landmark.

Table 3. Learning scores obtained by normal and operated monkeys on the spatial discrimination task with asymmetric landmark.

Groups	<u>n</u>	Mean trials	Mean errors
Normal control	5	288	69.80
Bilateral fornix	4	198	40.25*
Hippocampal	7	185	34.28*

Note: * Operated groups of monkeys made significantly fewer errors to learn the task than did monkeys in the normal control group ($p < .05$).

The results obtained with the asymmetric landmark, were unequivocal. Operated monkeys, without a single exception, learned the task in fewer trials and errors than did normal monkeys. The critical factor in this task seemed to have been the structural asymmetry of the landmark itself, which lent it an orientation in space, and which did not depend upon the superimposition, or extrapolation, of egocentric frame of reference as seemed to occur with the cylindrical (symmetric) landmark used in the first landmark experiment.

The present study constituted the first attempt to assess the role of visual landmarks in the spatial learning of monkeys with selective ablations of the hippocampus. Findings from two earlier studies in which landmarks were used (Pohl, 1973; Ungerleider and Brody, 1977), indicate a posterior parietal cortical locus as the most important brain area mediating landmark discrimination learning. Our results supplements the information obtained in those studies by demonstrating that another brain region heavily implicated in spatial cognition, namely the hippocampal formation, appears uninvolved in allocentric spatial learning.

Even though the two landmark discrimination tasks were not designed within the context of O'Keefe and Nadel's (1978) theory of hippocampal function, the results obtained with these two tasks are consistent with one prediction derived from that theory: Namely, that animals deprived of the hippocampus can still learn about space by using guidance (or orientation) route learning strategies within the taxon system. However, in view of the great experimental sophistication of monkeys in the present study, and of the differential effects of early and late ablations of the hippocampus on other behavioral functions, the definitive test of that hypothesis must await the postoperative administration of the landmark task to older hippocampectomized monkeys.

Trial-unique position recognition task

Up to this point in this follow-up investigation, we had found that monkeys with ablation of the hippocampal formation were initially impaired, and later recovered, the ability to learn a spatial discrimination on the basis of egocentric cues (spatial reversal, delayed alternation). We also had found no impairment, and even facilitation, in these monkeys spatial learning when distinctive allocentric cues were provided (landmark discrimination tasks). A next step was to devise a task, which could not be solved with the use of either egocentric (i.e., left-right, distal-proximal, up-down), or allocentric (i.e., guidance, orientation) spatial strategies. In order to avoid providing monkeys the benefit of a constant relationship between a given spatial location to be discerned and their body or a salient sensory cue, on or outside the tray, the new task required the use of trial-unique location in testing space. Similar to the object-recognition memory task these monkeys had seen before (Mahut and Moss, 1985), this task would assess the monkey's capacity to distinguish, after a single previous experience, a familiar from a novel of two identically marked positions on the tray. Thus, performance on the position recognition task depended on the availability of a representation (map) of the testing space, so that responses not given before, nor prescribed by the representation, could be correctly generated. As already mentioned, the position recognition memory task contained important spatial as well as memory component, and therefore, it was particularly appropriate to assess spatial function in monkeys with bilateral section of the fornix which, we knew, were unimpaired on the recognition memory test with objects (Mahut and Moss; 1985; Rehbein, 1985; 1991).

As was the case in previous testing, monkeys were tested in a modified Wisconsin General Testing Apparatus. The same tray containing three rows of six wells, used in first landmark task, was used. Two identical aluminum discs, 4cm in diameter, mounted on brown plastic rims were used as food covers. As illustrated in Figure 3, any given trial consisted of covering the bait contained in one of the 18 wells (sample position) and allowing the monkey to retrieve it by displacing the disc. This was followed, 10 seconds later, by the opportunity to choose between the sample position (now containing no food reward) and a novel position (now containing the food reward). An illustration of the testing situation is presented in Figure 3.

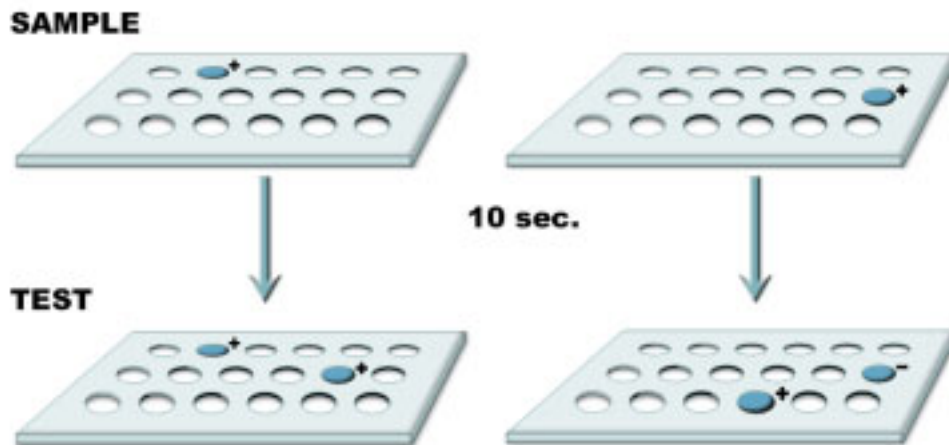


Figure 3. Illustration of the procedure used in the position recognition memory task with examples of two trials. “+”: Denotes presence of food reward. “-”: Denotes absence of food reward.

Five different sequences of 20 pairs of positions were semi-randomly selected from a listing of all possible combinations of 2 positions on the tray. Near-far and left-right sample positions vis-à-vis novel positions were counterbalanced within each session. Twenty trials a day were given and monkeys were trained until a learning criterion of 90 correct responses in 100 consecutive trials was met, or to a maximum of 1000 trials. Following the basic task with 10 sec delays, intervals between sample and recognition test trials were increased in stages to 30, 70 and 130 seconds, for a total of 140 trials with each delay.

Control monkeys learned the task in 400 to 720 trials with an average of 148 errors. In contrast, all monkeys in group H failed to learn the task within the limits of testing, and reached an average of only 72% correct response level in the last 100 trials. Three of the four monkeys in group BF learned the task within normal range.

With delays of 30-, 70- and 130-sec, monkeys in group H performed at significantly lower levels of accuracy than did monkeys in groups N and BF. Performance of monkeys in group BF did not differ from that of normal control monkeys, except at the longest 130' interval. These data are illustrated in Figure 4.

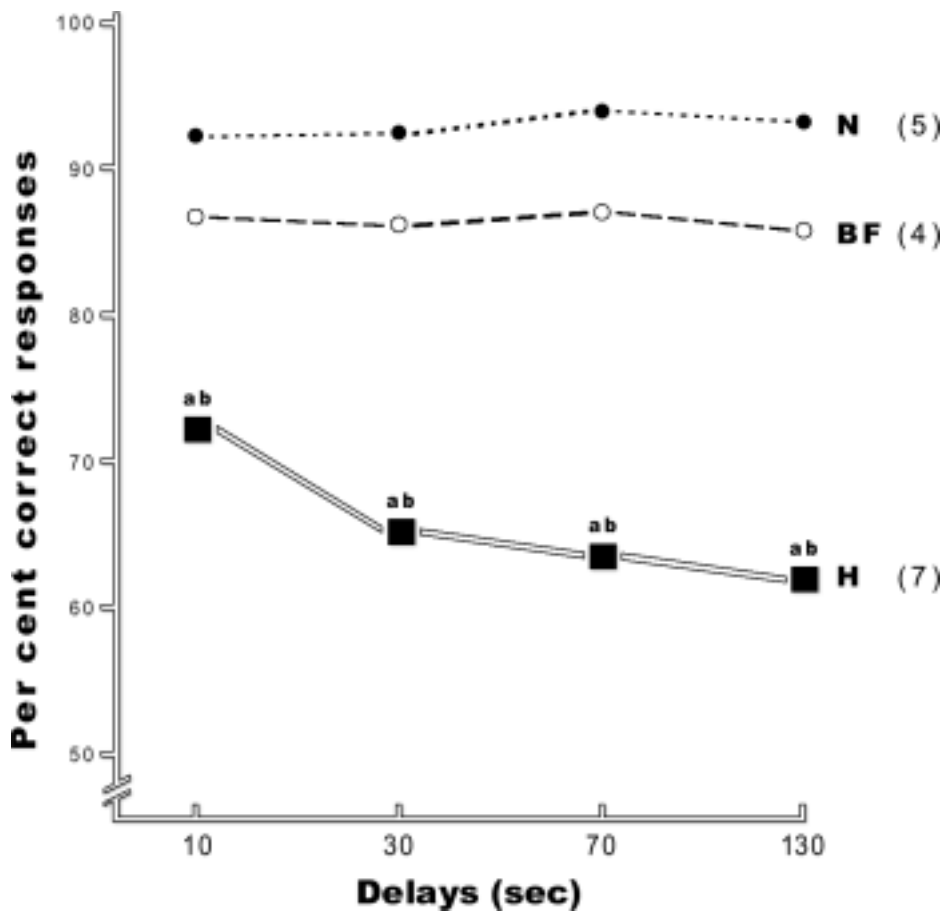


Figure 4. Mean group accuracy attained by four groups of monkeys in the position recognition memory test with delays. Larger solid symbols indicate significant group differences ($p < 0.05$). Letters a and b, show that significant differences were found versus either the Control (N), or the Bilateral fornix (BF) group, respectively.

This experiment provided direct evidence of recovery of spatial function in monkeys with early bilateral sections of the fornix. Performance of monkeys in group BF had been postoperatively impaired on the spatial reversals task, but had recovered by the third administration of that task, two

year after surgery. Performance of these monkeys on the delayed alternation task was also found unimpaired, 5 to 6 years after surgery (see above).

However, the latter result was inconclusive in view of the similarity between the spatial reversals task, in which they had had extensive practice, and the delayed alternation task. Therefore, these monkeys lack of impairment in the position recognition memory task, in spite of its memory component is a strong indication that recovery of spatial capacity in these monkeys was unspecific. This experiment also demonstrated a long-lasting deficit in spatial memory function in monkeys with early hippocampal resections. In spite of their improved performance on the last retest with the spatial reversal task, two years after surgery, and the absence of group impairment on the delayed alternation task, five years after surgery, they were severely impaired on a task, which required trial-unique delayed position recognition, as late as seven years after surgery (Rehbein, 1985).

Recognition memory span tasks: Positions vs. Objects

In view of the long-standing impairment shown by monkeys in group H on either nonspatial, or spatial, trial-unique memory tasks (Rehbein, 1985; Mahut and Moss, 1985), a different recognition memory test was designed which offered two novel features: First, unlike in most tasks presently in use to assess memory capacity in the monkey, it was not the experimenter who, by increasing the delay or adding items to a list, would set the difficulty of the task. Instead, in the new task, it would be, presumably, the monkey's own immediate memory capacity what would determine the limit of performance. Second, by using constantly changing sequences of items, the new task would allow to test memory for the incidental repetition of one, and the same, sequence of stimuli.

As mentioned earlier, this method for testing memory was originally designed by Hebb (1961) who found that human subjects improved their recall of a recurring sequence of digits, whereas no significant improvement was observed in their recall of nonrecurring ones. That finding has since been taken to demonstrate that, even within the context of immediate memory processes, there is already a more permanent, perhaps structural change in the memory trace (Hebb, 1961). In our adaptation of Hebb's (1961) experiment, monkeys were presented series of a small set of either highly familiar positions, or objects, from which a single series was repeated on every fourth trial. On this task, we considered it of interest to see (i) the number of items normal, control monkeys would be able to hold in immediate memory (recognition 'memory span'); (ii) if as in normal humans, the memory of normal monkeys would improve with repeated, relative to nonrepeated series of stimuli; and (iii) if in spite of an expected reduced memory span, the 'Hebb effect' would also be found in monkeys with ablation of the hippocampus. If the latter were found, it would provide support for long-term memory processes that would operate outside the hippocampus. Of additional interest would be the assessment of possible differences in performance relative to the spatial, or nonspatial, nature of the stimuli to be remembered.

Testing with position series. Testing took place in a modified Wisconsin General Testing Apparatus, and the same 18-well tray used in the previous experiment was used. Identical aluminum discs, 4cm in diameter, mounted on brown plastic rims were prepared as food covers. From the eighteen possible positions on the tray, two complementary sets of 9 target positions were selected such that at no axis would they be adjacent to each other, except at the diagonal one. On the basis of these two sets of positions, 25 different sequences of 9 positions each were built by using a table of random digits. On any given day, monkeys were shown the first position of a series with one of the aluminum discs covering an M&M chocolate candy, or other highly preferred food. Following the retrieval of the bait, the opaque screen was lowered, the same position was re-covered and the second position in the series was baited and covered with another disk. The same procedure was used for the subsequent positions in the series with an interval of approximately 5 sec between the covering of two successive positions. Presentation of positions within a series was terminated at their first error (i.e., the first time the monkey failed to uncover the most recently covered position). Each daily session consisted of a single presentation of two different series with an interval of 15 sec in between series. The second series presented on every other day of testing was always the same series (repeated). Series in between the repeated one were always different (nonrepeated). Testing was continued for a total of 32 sessions, or for 48 nonrepeated and 16 repeated series. The results obtained with repeated and nonrepeated position series are illustrated in Figure 5.

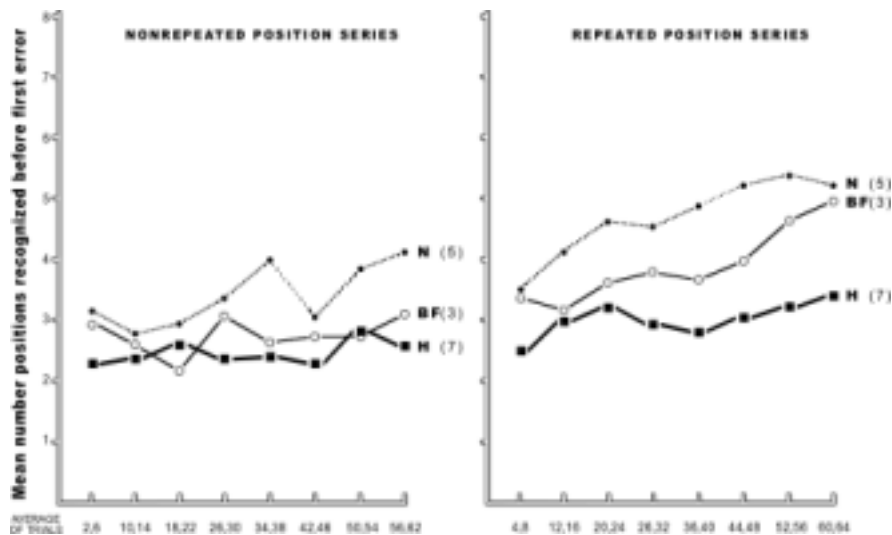


Figure 5. Performance of normal and operated groups of monkeys on the recognition memory span task with non-repeated and repeated position series.

When tested with position series, monkeys in group N reached a mean position recognition span of 3.72 (range 1-9) in nonrepeated, and 4.61 (range 1-7) in repeated series. In contrast, monkeys in group H reached a mean position recognition span of 2.35 (range 1-6), and 2.96 (range 1-6), with nonrepeated and repeated series, respectively. For monkeys in group BF, the mean position recognition span was 2.80 (range 1-7) with nonrepeated, and 4.45 (range 1-7) with repeated series.

A posteriori comparisons made between each group's initial and final performance showed the position recognition span of monkeys in group N, increased significantly during testing with nonrepeated and repeated series; whereas no significant differences were found between the initial and final position recognition span of monkeys in group H. In turn, performance of monkeys in group BF did not improve significantly with nonrepeated position series, but their performance did improve significantly by the end of their testing with the repeated position series.

Testing with objects series. After 32 days of testing with positions, a similar procedure was followed using a set of 15 small, distinct objects to cover the wells. Twenty-five series of positions, different from the ones used in the spatial form of the task, were prepared. Objects were numbered and pre-assigned to the sequence of positions in each trial by using a random digit table. Thus, each sequence consisted of specific objects in specific positions, and these were changed from one trial to the next, except for every fourth, repeated, series in which order of objects and positions were always the same. Monkeys were tested for 32 days on this version of the task, or for a total of 48 nonrepeated and 16 repeated series.

Re-test with position series. Immediately following the recognition memory span test with objects, monkeys were re-tested for an additional 10 days with nonrepeated position series, as a control for possible order of tasks effects.

The mean object recognition span of monkeys in group N was 6.80 (range 1-12) with nonrepeated, and 6.57 (range 3-10) with repeated object series. In contrast, monkeys in group H -attained a mean object recognition span of 3.20 (range 1-8), and 3.51 (range 1-8) with repeated and nonrepeated object series, respectively. The object recognition span of monkeys in group BF was 4.10 (range 1-8) with nonrepeated, and 4.69 (range 3-7), with repeated object series.

Similarly to what was observed with position series, the operated groups of monkeys attained a significantly smaller object recognition span than did the control group of monkeys. Comparisons between each group's performance on the first and the last 12 days of testing (first and last 3 points on the curves in Fig. 6), showed that monkeys in groups N and BF had significantly increased their object recognition span with training on

nonrepeated and repeated object series; whereas no significant increase was found in the object recognition span of monkeys in group H, as a result of training both with nonrepeated and repeated object series. (Rehbein, 1985; 1991).

The results obtained with the recognition memory span task demonstrated, first, that normal monkeys were able to increase their recognition memory span in all four conditions. Overall, this increase was less pronounced with position than with object series, in which normal monkeys quickly reached, and stabilized, at a span of 7-8 cumulatively recognized objects. Second, normal monkeys also showed a significantly greater recognition span increase with repeated, than did with nonrepeated position series. However, no differential increase was observed in their recognition span with repeated and nonrepeated object series, possibly because they were already at the limits of their immediate memory capacity.

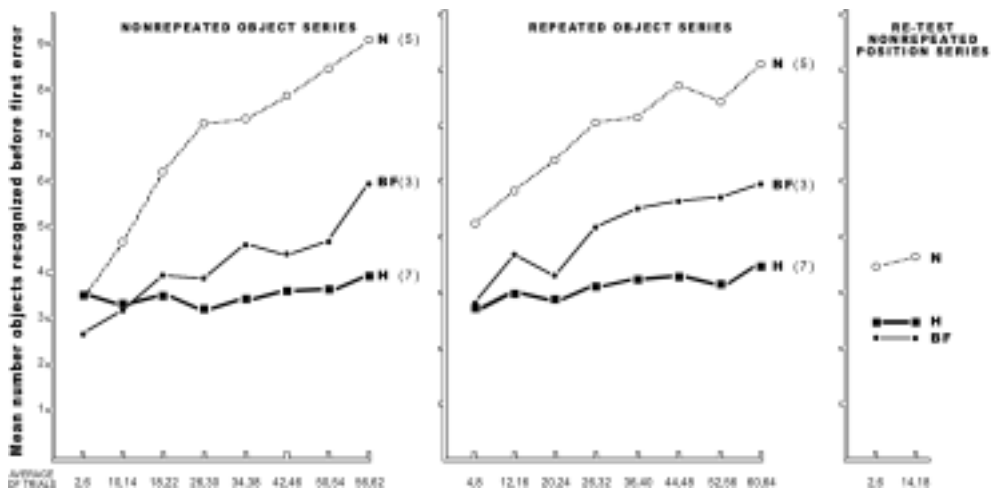


Figure 6. Performance of normal and operated groups of monkeys on the recognition memory ‘span’ task, with repeated and non-repeated object series.

The recognition memory span of monkeys in group BF was always between that of monkeys in groups N and H. Whereas this group of monkeys increased its recognition span with training on repeated, as opposed to nonrepeated position series, only monkeys in group BF, as did those in group N, obtained a bigger span with object, as opposed to position series. That differences between object and position series observed in the recognition span of groups N and BF were not due to the order in which the two stimulus conditions were presented, or to the total time on training, was demonstrated by the corresponding decrease of the recognition span on the re-test with position series (Rehbein, 1985a).

Third, unlike normal monkeys and those with fornix damage, monkeys in the hippocampal group did not increase their recognition span either as a function of training, repetition of the same series, or the use of multidimensional objects instead of identically marked locations. Thus, this experiment confirmed and extended the finding of severe spatial memory deficits after hippocampal damage obtained with the position recognition task with delays in the previous experiment. Only, this time, the deficit was reflected by the inability of monkeys in group H to recognize more than 2 to 3 items at the time as familiar, in spite of extended training.

An adaptation of the recognition memory span task has been successfully used to assess memory loss in patients with different degenerating brain diseases (Moss, Albert, Butters, and Payne, 1986); to assess memory in aging monkeys (Moss, Killiany, Lai, Rosene, and Herndon (1997); and more recently, to assess developmental changes of recognition memory span in children (Rehbein, Barría, Massardo, Oyarzún and Schade, 2002).

Some evidence from experimental field studies

Though it is not the goal of the present article to review all of the literature on spatial learning and memory function in intact free-ranging animals, we nonetheless thought it would be of interest to the reader to include some selected references to this interesting and challenging area of research. In contrast to laboratory studies, ecological approaches to the study of spatial learning have been very much associated to the study of the evolution of sensory capabilities and foraging behavior (Garber and Paciulli, 1996; Manzel, 1973;1991). In order to forage efficiently, an animal must be able to retain and integrate information regarding changes in the spatial and temporal availability of food resources. The information available to the forager, however, is likely to vary based on food type, the size and quality of the food patches, resource predictability, the presence/absence of potential competitors and predators, and its own cognitive skills.

In the case of nonhuman primates, data from both captive and field settings offer evidence of species-level differences in foraging patterns, and the degree to which individuals and groups use vocal, visual, olfactory, and spatial information to coordinate travel and locate feeding sites. In most instances, however, there is little direct information on how feeding sites are located, and whether species differ in their hierarchical or ordered use of spatial information. This scarcity of information seems to be a consequence of the fact that traditional methods in primatological field research have rarely included the level of controlled experimental design required to test hypotheses regarding problem-solving skills and spatial learning under natural conditions. Experimental field studies, however, offer an opportunity to control the level of environmental information available to the forager, and to examine directly species "differences in spatial learning, the development of foraging rules, and the hierarchy of perceptual cues used.... in making foraging decisions". (Garber and Dolins, 1997).

Despite a large body of data on diet and ranging patterns in prosimians, monkeys, and apes, little is known regarding the types of information that nonhuman primates use when making foraging decisions. In a series of controlled field experiments, Garber and Paciulli (1997) tested the ability of wild capuchin monkeys to remember the spatial positions of 13 feeding platforms and use olfactory and visual cues to identify baited (real bananas) versus sham (plastic bananas) feeding sites. The results indicate that when 'place' was predictable, the capuchins learned the spatial locations of food and nonfood sites rapidly (one-trial learning). In a second experiment, the positions of baited feeding sites were random. In the absence of other information, the capuchins used the presence of a local landmark cue (yellow block) placed at reward platforms to select feeding sites. The results also show that expectations regarding the amount of food available at a platform (2 bananas vs. 1/2 banana) had a significant influence on capuchin foraging decisions. Although the capuchins were extremely sensitive to changes in experimental conditions, when given conflicting cues, spatial information was predominant over other information in selecting feeding sites.

In another study, MacDonald, Pang and Gibeault (1994) explored the spatial memory of captive common marmosets through 3 experiments using a simulated foraging task. In the first experiment, individual monkeys foraged among 8 baited food sites. They appeared to use spatial memory to accurately avoid revisiting previously depleted sites. There was no difference in accuracy between the adult monkeys and a juvenile monkey tested on the same task. In the second experiment, a win-stay paradigm was used. The adult monkey subject remembered very accurately the locations that had previously contained food. The monkey tended to visit adjacent correct sites when retrieving food and thus minimized the total distance traveled. In the third experiment, a win-shift paradigm was used with 2 adult monkeys. Although both monkeys performed at above-chance levels of accuracy on the win-shift task, they made many errors. These results suggest that marmosets may prefer tasks that require a win-stay strategy. Also, they appeared to be attracted to sites where a social partner was either searching for or discovering food, which is known as a local enhancement effect. For marmoset monkeys, who forage in family groups, all members of the group will be quickly drawn to a food site discovered by one animal, thus ensuring that all group members benefit.

With a similar rationale, Gibeault and MacDonald (2000) examined the spatial memory and foraging behavior of 6 western lowland gorillas living in captivity as a family group. Sixteen food sites were placed throughout the subjects' enclosure; while other subjects were kept apart; a mother-offspring pair freely visited the sites and collected food. Collected data included the order in which the gorillas visited the sites and recordings of aggressive displays and fighting. Results show that the foraging behavior of each subject was strongly dependent on the behavior of its partner. Five subjects were highly accurate in finding food. Subjects commonly used an adjacency pattern to find food, but this strategy was inconsistent. Each animal visited only a proportion of available sites; while they watched each other closely and avoided visiting sites together. It is concluded that subjects competed to

maximize their foraging efficiency, and exhibited a highly developed level of spatial memory in remembering which sites they and their partners had depleted. In addition, access to food was often physically fought over. Interestingly, and quite contrary to what was seen in the marmoset monkey, gorillas (as do also orangutans) have no inclination to share food with other members of the group.

In a somewhat more structured setting, Sutton, Olthof and Roberts (2000) studied the behavior of two squirrel monkeys in search for a reward buried in one of 144 holes that formed a 12 X 12 grid (48 X 50cm). An array of vertical, colored landmarks was placed on the grid, and their locations on the grid were changed from trial to trial. During successive training conditions, the mealworm reward was placed either in the center of a square array of landmarks, or midway between two landmarks. On nonrewarded test trials, the monkeys searched among landmarks placed in the same arrays as those used in training and among landmarks placed in an expanded array, or in an array intermediate between the two arrays used during training. Distributions of searches on test trials indicated that the monkeys searched mostly within the configuration of the landmarks, but that they had not coded the location of the reward as being either in the middle of the landmarks, or at a fixed distance and direction from a given individual landmark.

It is evident that new research on spatial cognition of primates (as well as that of other species) performed in ecological and natural settings is yielding increasingly more interesting and complex information; and that it would be instructive to compare these results with findings and theories generated from the laboratory.

Brain mechanisms involved in spatial behavior

Taken together, the findings reviewed here suggest that spatial information is coded with respect to more than one frame of reference; and therefore, spatial information cannot be specified in absolute terms, but must always be defined relative to some set of coordinates or frames of reference. The hippocampus and the parietal cortex have been implicated in various core spatial behaviors, such as the ability to localize an object and navigate to it, since damage to these areas in humans and animals leads to impairment of these spatial functions.

Contrary to this notion, the claim that space is represented in absolute coordinate systems is based, in part, on arguments by O'Keefe and Nadel (1978). They presented physiological evidence that the mammalian hippocampus is specialized for coding place in absolute allocentric space. Feigenbaum and Rolls (1991) have recorded individual hippocampal neurons that respond to allocentric position, although their data can also be interpreted to support the idea that body axes can serve as a frame of reference, just as allocentric coordinates do. Some evidence for this comes from studies by Farah et al. (1990) showing that attention to locations in space is allocated with respect to both allocentric and egocentric frames of reference. In addition, Kesner, Farnsworth, and DiMattia (1989) report evidence that areas in the

mammalian frontal cortex are specialized for organizing egocentric cognitive maps. Tamura, Ono, Fukuda, and Nakamura (1990) have found hippocampal neurons in mammals that respond to locations in the egocentric frame of reference.

It was clearly not the objective of this paper to review the enormous amount of research this area has attracted in the last few years; not to mention the last few decades. However, we have chosen to mention at least some of the authors who have contributed with significant research in the area, just to serve as a starting point for those readers who might be interested in pursuing their inquiry further. In such spirit, it is of interest to mention the compilation of remarkable contributions, recently published by Burgess, Jeffery and O'Keefe (1999). Amongst several outstanding chapters there is the one by Olson, Gettner and Tremblay (1999) where they describe how the allocentric and egocentric frames of reference provided by the hippocampal and parietal systems are complemented by object centered frames of reference from the supplementary eye fields of monkeys.

The work of authors with longstanding and significant contributions in this field, like those of Mortimer Mishkin, Larry Squire, Stuart Zola and others, has been thoroughly reviewed by Mark Good in a previous paper in this issue.

Additional work towards fractioning the effects of temporal lobe damage, and identifying the physiologic function of the rhinal cortices in particular, has seen major advances in recent years (e.g., Suzuki, Miller and Desimone, 1998; Murray, Baxter and Gaffan, 1998; Miller and Desimone, 1994). Most of these findings argue against the idea that the mnemonic contributions of the rhinal cortex and hippocampus are circumscribed to object and spatial domains, respectively.

Interestingly, in spite of the reviewed behavioral evidence, which seems to cast a doubt to the claims about the central role of the hippocampus in trial-unique object and place recognition memory, there is a reaffirmation of such a role coming from some recent single-cell recording studies. Thus, a report by Rolls (1999) presents neurophysiological evidence of how space is represented in the primate hippocampus and how this is related to memory and spatial functions of the hippocampus. Information represented in the primate hippocampus was analyzed by making recordings in monkeys actively walking. In a sample of 352 cells recorded, no place cells were found, but a considerable population of spatial view cells was found that tuned to respond when the monkey looked at small parts of the environment. Research has demonstrated: (1) these hippocampal neurons respond to a view of space, not to the monkey's location; (2) responses depend on where the monkey is looking; (3) responses in some cases (e.g., CA1 but not CA3) still occur if view details are obscured; (4) cells retain part of their space tuning even in darkness, for several minutes; and (5) spatial representation is allocentric. This representation of space by primate spatial view cells would be an appropriate part of a system involved in memories of particular episodes of where in an environment an object was seen. Spatial view cells (in conjunction with whole

body motion cells in the primate hippocampus, and head direction cells in the primate presubiculum) would also be useful as a memory component in a spatial navigation system.

Using similar electrophysiological recording techniques, Matsumura and collaborators (1999) studied the functional significance of the monkey hippocampal formation (HF) and parahippocampal gyrus (PH) neurons in allocentric spatial processing during the performance of spatial tasks. On the tasks, the monkey either moved freely to 1 of 4 reward areas in the experimental field by driving a cab that the monkey rode (real translocation task), or it moved a pointer to 1 of 4 reward areas on the monitor by manipulating a joystick (virtual translocation task). Of 389 neurons recorded from the monkey HF and PH, 166 had place fields that displayed increased activity in a specific area in the experimental field and/or on the monitor (location-differential neurons). More HF and PH neurons responded in the real translocation task. Furthermore, these authors found that most location-differential neurons showed different responses in different tasks. These results suggest that the HF and PH are crucial in allocentric information processing and, moreover, that the HF can encode different reference frames that are context or task-dependent. This may be the neural basis of episodic memory.

Another brain area that has long been implicated in spatial function is the frontal cortex. In fact, previous work in nonhuman primates and in patients with frontal lobe damage has suggested that the frontal cortex plays a critical role in the performance of both spatial and nonspatial working memory tasks. In a recent study Owen, Evans and Petrides (1996) used positron emission tomography with magnetic resonance imaging to demonstrate the existence, within the human brain, of two functionally distinct subdivisions of the lateral frontal cortex, which may subserve different aspects of spatial working memory. Five spatial memory tasks were used, which varied in terms of the extent to which they required different executive processes. When the task required the organization and execution of a sequence of spatial moves retained in working memory, significant changes in blood flow were observed in ventrolateral frontal cortex (area 47) bilaterally. By contrast, when the task required active monitoring and manipulation of spatial information within working memory, additional activation foci were observed in mid-dorsolateral frontal cortex (areas 46 and 9). These findings support a two-stage model of spatial working memory processing within the lateral frontal cortex.

In a study using monkeys with either orbitofrontal or anterior cingulate lesions, Meunier, Bachevalier, Mishkin (1998) assessed object memory processes with a trial-unique delayed nonmatching-to-sample and an object reversal learning task. They found that monkeys with orbital frontal lesions were more severely impaired than those with anterior cingulate lesions. Spatial memory process assessed by spatial delayed response and spatial reversal learning showed a weak trend in the opposite direction, though on these tasks neither lesion produced a serious loss. When comparing these results with those from earlier studies on the effects of various limbic system lesions, it appears that object memory processes, including object recognition

and object-reward association, are served by a circuit consisting mainly of the rhinal cortex, orbitofrontal cortex, and the magnocellular division of the mediodorsal thalamic nucleus. Although both the rhinal and orbitofrontal components of this circuit appear to participate in both functions, evidence from this and earlier studies suggests that the orbitofrontal component is the more important one for associative memory, (i.e. the formation across trials of associations between particular objects or classes of objects and reward), whereas the rhinal component is the more critical one for recognition memory, i.e., the storage and retrieval within trials of the representations of particular objects. These inferences, though they must be taken with caution, appear to be grossly congruent with our own earlier findings (Rehbein, 1985; Mahut and Moss, 1985).

CONCLUSIONS

The first important conclusion to be drawn from the initial set of studies discussed in the first section of this paper is that the improved performance of monkeys with early hippocampal damage on left-right discrimination tasks, and their facilitated spatial learning in the presence of allocentric landmarks, did not reflect a recovery of their general spatial capacity. This was demonstrated by their profound impairment on the trial-unique position recognition task and on the position recognition span task. This finding was not surprising in view of these monkeys' known impairment on other trial-unique memory tasks (Rehbein, 1985; Mahut and Moss, 1985). However, the mnemonic deficit reported with the object recognition test in those studies appeared to be greatly exacerbated in the present study by the spatial nature of the stimuli used.

Unlike in left-right discrimination learning or in landmark guided behavior, in the position recognition task monkeys could not be helped by either egocentric, or allocentric, cues since on every trial the novel position could appear on anyone of 17 locations, which could be 360 degrees around the sample position, and which bore no constant relationship with salient sensory cues outside the tray. Instead, correct performance in the position recognition and recognition span tasks depended on the availability of a representation (map) of the 18 positions on the testing tray, so that responses that were not foreseen nor prescribed by the representation (i.e., responses to novel positions within a given trial) could be correctly generated. Thus, in fact, the trial-unique position recognition and the position recognition span studies, represent an exploration of a third, distinct mode of spatial cognition, different from those involving 'egocentric' or 'allocentric' spatial strategies explored in the first three experiments. It is this capacity for establishing a representation of the spatial features of the environment which has been proposed by O'Keefe and Nadel (1978) as the primary function of the hippocampus. Interestingly, it was also this capacity which appeared most affected in our monkeys with hippocampal damage, in spite of the sophistication arising from 6 years of nearly uninterrupted training on a wide variety of tasks.

However, in spite that results from the present study lent support to at least two important predictions derived from O'Keefe and Nadel's (1978) theory of hippocampal function, (i.e., hippocampal damage left intact the use of guidance hypothesis in the landmark experiments, but impaired spatial mapping in the experiments that required trial-unique position recognition), we have reasons to question the exclusively spatial role of the hippocampus advanced in that theory. For example, we have consistently found hippocampal damage also to impair nonspatial tasks with trial-unique stimuli (Mahut et al., 1982; Rehbein, 1985). These findings suggest a more encompassing, cognitive-mnemonic involvement of the hippocampus than that proposed by O'Keefe and Nadel (1978). In fact, the bulk of our findings can be best understood in reference to the theoretical postulates of Hirsh (1974; 1980). In his view, there are at least two neural systems, which can mediate complex learning. One is a cognitive learning system which uses conditional information arising from stimulus configurations, motivational states or items stored in memory, and the operation of which depends on the integrity of the hippocampus. The other is an associative learning system, based on the gradual strengthening of S-R bonds as a function of repeated reinforcement, the operation of which depends on neural systems other than the hippocampus (See Hirsh and Krajden, 1982, for a characterization of the two systems).

The second major conclusion to be drawn from this review stems from the area of experimental field research with nonhuman primates. There is a growing body of evidence both, from captivity and the wild, which has an enormous potential to feed into the discussion and theorizing based on laboratory and neuropsychological data. In spite of the difficulty of running experimental research in open field or ecological settings, we are convinced that controlled field experiments offer a powerful tool for studying spatial problem solving and learning. We also believe that cross-fertilization of ideas between this emerging field and laboratory research on spatial cognition might be of great benefit for all investigators involved.

The third, and final conclusion that can be drawn here is that the study of brain mechanisms of spatial cognition is a very prolific area of research, which keeps attracting and engaging experimental psychologists and neuroscientists from different disciplines. However, in spite of the explosive growth observed in this area during the past few years, there is still no unequivocal evidence as to how various brain regions interact to integrate and process information leading to spatial behavior. In fact, what is becoming ever more clear, is that when adaptive behavior is performed, several egocentric-allothetic transformations are required; and therefore, that different brain areas need constant coding and re-coding (up-dating) in multiple frames of reference. Which brain structures or regions are responsible for the function of organizing attention, perception, intention and action in frames of reference that can allow an organism to interface its actions with objects in the outside world? These, more integrative sort of questions, must await further research and discussion, before we are able to articulate an answer.

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