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Research report

Problem solving and logical reasoning in the macaque monkey

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Abstract

This study focuses on the performances of monkeys in a spatial problem-solving task that involves working memory. Two monkeys had to find, by trial-and-error, the touching order of 2 or 3 targets in a set of 3 or 4 fixed spatial targets. When a solution was found and performed 6 times, the order was changed and the animal had to resume a new search within the same set of targets. Thus, in a training session, many searches (up to 60) could be initialised. The data show that the animals conducted a methodical search for the hidden order and found the solution in a minimal number of trials. We conclude that the monkey is able to construct complex cognitive structures, similar to logical reasoning, to solve spatial problems of this type.

Keywords: Problem solving; Logical reasoning; Monkey; Working memory

1. Introduction

The processes underlying the higher cognitive functions, working memory, mental imagery and willed action require that information be held in mind for a period of time. Our approach to the working memory in monkey is to study the faculty to hold representations, but also to manipulate these representations. Holding and manipulating information are critically important in cognitive acts such as planning or problem solving.

The planning abilities have been studied in the monkey in particular in sequential motor tasks. It has been shown that the animals can develop motor strategies [2,8,12,14]. A behavioral strategy includes the goal and the temporal organisation of individual acts that are in accord with it and with a variety of intervening events. Animal studies support the idea that novel, complex and temporally extended motor plans are formed and stored under the control of prefrontal cortex [6,7].

To analyze the elaboration of complex motor plans in animals, the present study evaluates the abilities of two macaque monkeys engaged in a spatial problem solving task. The task consisted of finding, by trial-and-error, the correct order of touching 2 or 3 targets in a set of 3 or 4 fixed spatial targets. It requires that the animal memorises, from one trial to the next, the position and the rank of the correct touches and rejects the incorrect ones. When the solution was found, the order was changed and the animals had to start a new search. Eye movements were recorded. The data show that the monkey is able to conduct a methodical search for the hidden order and to find the solution in a minimal number of trials.

2. Materials and methods

2.1. Animals and materials

Two male rhesus monkeys, 3 and 4 years old, weighing 5 and 7 kg, were trained. They were seated in a primate chair in front of a tangent touch-screen (30×40 cm) coupled to a TV monitor (Microtouch System), in a sound-attenuating box. The screen was located at arm's reach (approximately 21 cm from the eyes). In the front panel of the chair, an arm-projection window (10×10 cm) was opened, and allowed the monkey to touch the screen with one hand. A PC 486 DX 33 computer recorded and controlled the correctness of each touch of the monkey on the touch-screen. It also controlled the presentation of visual stimuli on the

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monitor (2 × 2 cm grey or white squares) which served as light targets.

In one series of experiments, the animal worked with 3 targets. One was located 7.5 cm above centre of the screen; two lower targets were located 7.5 cm to the right and to the left and 7.5 cm below centre. In another series of experiments, 4 targets were used. Two upper targets were located 5.5 cm to the right and to the left and 4 cm above centre; two lower targets were located 7.5 cm to the right and to the left and 7.5 cm below centre. In both series, a 3 × 3 cm white square located 10 cm below the centre served as the starting lever.

Eye movements were recorded with the scleral search coil technique, using two magnetic fields oscillating at separate frequencies of 45 and 67 kHz (Skalar, eye position meter 3010). They were digitised at 250 Hz. The personal computer recorded touches, visual events and eye movements on the same time scale.

2.2. Behavioural paradigm

The animals were trained on two tasks: a visually guided sequence task; and a non-guided sequence task.

2.2.1. Visually guided sequence task

In the visually guided sequence task (Fig. 1A), the animals worked with 3 targets. They had to memorise the presentation order of 2 targets and, after a delay, had to touch them in the same order. To start a trial, the monkey touched the lever; the lever disappeared and the animal kept its hand on the corresponding position. This started an instruction period of 3.5 s. During the period, two targets were illuminated 'grey' for 500 ms consecutively at 500 and 1500 ms. (When the animal worked head-fixed, a 5 × 5 mm central white square appeared on the screen and served as a fixation point for the gaze until its extinction at the end of the period). At the end of the instruction, the execution period began. All 3 targets were simultaneously illuminated 'grey' for 1.5 s. When their colour turned 'white' (white period = 'GO' signal), the animal had to release the lever and touch the target that had been illuminated first. Immediately after the first touch, all 3 targets were simultaneously re-illuminated at standard level (grey) for another 1.5 s, while the monkey kept its hand on the first target. Then, the targets turned white again and the animal had to touch the second target. Immediately after each correct touch, a short tone was delivered to the animal from a buzzer located above the screen. If the monkey performed the task correctly, it was rewarded with a squirt of apple juice.

The animal was presented with different sequences that were randomly selected by the computer between the 6 possible combinations. A trial was aborted in case of incorrect behaviour (no respect of the delays; incorrect target choice). A correction procedure (repetition of a sequence until it is successful) was adopted throughout the training sessions.

After several months of training, the monkey was familiar with the task of touching two targets in a row within the temporal constraints described above. It supposedly knew that 'order' was important. Then, it was trained on the non-guided version.

2.2.2. Non-guided sequence (problem-solving task)

In the non-guided sequence (problem-solving task) (Fig. 1B), the monkey worked with 3 or 4 targets. It had to discover, by trial-and-error, the pressing order of 2 or 3 targets. During the instruction period (2500 ms), all targets were simultaneously illuminated at times 500 for 500 ms. The execution period was the same as in the visually guided sequence. Each correct touch was signalled by a short tone. The correct trials were rewarded; the incorrect trials were aborted and the research process was repeated until it was successful. A time interval of

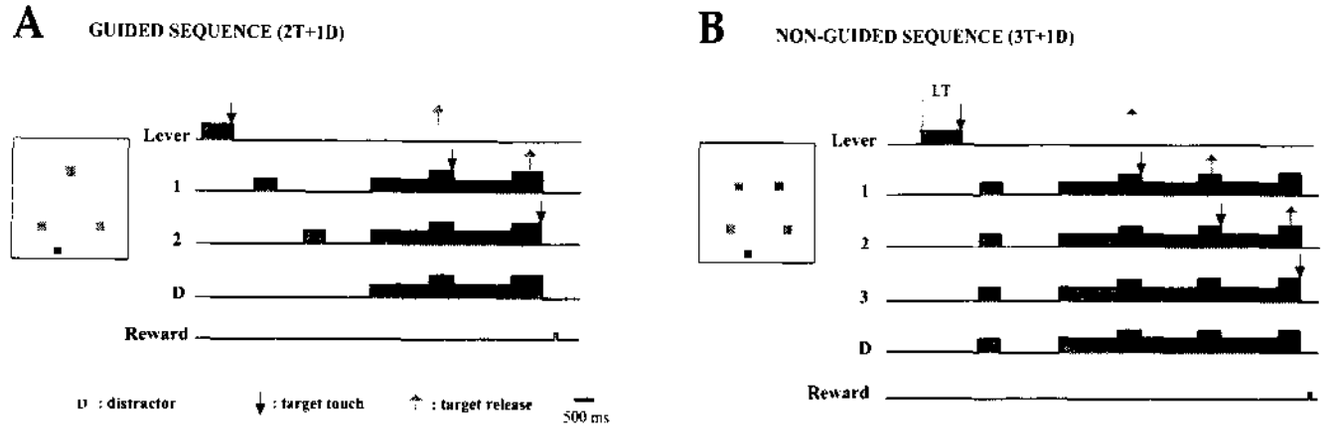


Fig. 1. Behavioural paradigms. Schematic representation of the set-up with 3 or 4 targets in the guided (A) and non-guided (B) tasks. Definition of the events. 1–3: notation indicating the rank of onset and/or of the pressing order of the targets. Grey area: time of illumination of the targets; higher amplitude in the grey area: full illumination (GO signal). See Materials and methods for details.

2 s separated the end of a trial and lever onset for the next trial.

The monkeys were first trained to find the pressing order of 2 targets in a set of 2. When the task was mastered, they were tested in the search process of 2 targets in a set of 3 (2 targets and 1 distractor = 2T + 1D) (Table 1). One monkey (monkey 2), was then trained and tested in the search for 2 targets in a set of 4 (2T + 2D) and 3 targets in a set of 3 (3T + 0D). When it mastered these tasks, it was tested in the search for 3 targets in a set of 4 (3T + 1D). In this task, 2 versions were administered to the animal. In one version (V1), after the second target of the sequence had been found, only the 2 non-hit targets turned bright for the next hit; the other targets remained dim; thus, the choice of the animal for the third target was artificially restricted to the 2 remaining non-pressed targets. In the second version (V2), all targets turned bright for the third hit.

In contrast to the visually guided trials, each sequence was repeated until the animal had performed a total of 6 correct trials. This repetition was aimed at studying the consolidation processes following the discovery of the correct order.

When the series of 6 correct trials was terminated, a central red circle was flashed 3 times on the screen and a tone was delivered through the loud-speaker, indicating a change of sequence to the animal. The different sequences were randomly chosen by the computer, under the condition that two successive sequences never had the same first target. There were 6 different sequences of 2 targets in the set of 3 targets, 12 sequences of 2 targets and 24 sequences of 3 targets in the set of 4. In each training session, which lasted approximately 2–3 h, each monkey initialised up to 60 searches.

2.3. Eye movements

When the monkey mastered the non-guided tasks, it was trained to work head-fixed and its oculomotor activity was controlled with a fixation condition. Our hypothesis was that, in a spatial task, the analysis of eye movements may give access to the cognitive processes associated with the construction of the solution. During the instruction period, the animal had to fixate the fixation point (FP) until its extinction; during the execution period, it had to fixate the selected target during 1000 ms preceding the GO signal. If the animal broke the fixations, the trial was aborted. Free oculomotor activity during a trial was only allowed during the 800 ms following extinction of FP or following a target press.

The monkeys worked 5 days a week. Monkey 1 worked with the right arm; monkey 2 with the left arm.

Table 1
Description of the non-guided tasks and definitions of parameters N and P

Conditions	Finding the touching order of:
2T + 1D	2 targets in a set of 3
3T + 0D	3 targets in a set of 3
2T + 2D	2 targets in a set of 4
3T + 1D	3 targets in a set of 4
Parameter N (Fig. 2)	Number of trials to discover a sequence
Parameter P (Fig. 3)	Probability of keeping the first correct target in the trial which follows its discovery

2.4. Surgical procedures

During a pause in the training sessions, the animal was surgically prepared using aseptic technique and under general anaesthesia to receive a scleral search coil. The animal first received an intramuscular injection of the neuroleptic chlorpromazine (largactil 1 mg/kg, i.m., Rhone Poulenc Rorer, France). Then, the anaesthesia was induced with Ketamine (Imalgene, 10 mg/kg, i.m., Lab Rhone Merieux, France) and supplemented with intravenous Propofol (Diprivan, i.v., Zeneca Pharma), diluted at 50% and delivered as necessary to maintain deep anaesthesia. During the surgery, the heart rate, pO_2 and temperature were continuously monitored.

The scleral search coil constructed with Teflon-coated stainless steel wire was implanted around the conjunctiva. A bar was fixed on top of the skull with small stainless steel screws and then embedded in an acrylic assembly to permit subsequent head fixation. After surgery and during 5 days, analgesic (paracetamol: Doliprane, 125 mg, UPSA) and intramuscular antibiotics (oxacillin: Bristopen 0.2 g/ml, i.m., Lab. Bristol, France) were given to the monkey to prevent pain and infection. Eyes were treated with local antibiotic and anti-inflammatory eye-lotion (Chibro-Cadron, Chibret). During all the postsurgical period, the head was daily cleaned with Betadine (Betadine scrub, Sarget) and treated with antibiotics (staphylomycin, Smith, Kline and French).

2.5. Data processing

In the visually guided sequences, performance was evaluated by the number (A) of correct trials compared to the number (B) of incorrect trials due to erroneous target choices. Errors due to no respect of the delays were not considered. The ratio R ($R = A/(A + B)$) characterises the performance.

In the non-guided sequences, two periods were analyzed: the search and the consolidation of the correct sequence. During the search period, 2 parameters were retained (Table 1): (1) the average number (N) of trials to discover a sequence. This number was compared to an optimal N obtained in case of a perfect logic and of a perfect memory. Optimal N depended on the sequence to find. In the case of search for 2 targets in a set of 4,

the solution is found between 1 (at best) and 6 (at worst) trials; thus, optimal N was 3.5. Optimal N in the different tasks is indicated in Fig. 2. (2) the probability (P) of keeping the first (correct) target in the trial which follows its discovery. This probability is a good measure of the animal's strategy. During the consolidation period, the average number of sequence losses (maximum 5 between the first and the last success) was calculated during each session. During the two periods, the time intervals between lever onset and monkey's lever touch (LT) were measured. Variations in these time intervals can reflect a specific haste of the animal at given stages of the search to test a hypothesis regarding the sequence or to consolidate a success. When the monkey worked head-fixed, different aspects of its oculomotor behaviour, in particular the duration of fixations, were also analyzed during the search and consolidation periods.

3. Results

Performance was estimated on the basis of experiments with head-free, whereas oculomotor activity was recorded in the head-fixed condition.

3.1. Guided sequences

After 5 months of training, monkey 1 performed 86% of the guided trials correctly (ratio R during the last 5 sessions). This corresponded respectively to a probability 0.96 and 0.90 to press the first and the second target correctly ($0.96 \times 0.90 = 0.86$). The performance dropped to 60% after training in the non-guided sequences. Analysis of the data in this case showed that the increasing number of errors was due to erroneous choices of the second target, as if the animal had adopted a strategy of trial-and-error for the second target, similar to that for the non-guided sequence.

Monkey 2 never achieved a good performance in the guided sequences. After 5 months of training his performance ranged between 50 and 72% of correct trials. The animal understood the significance of the first presented target, but not of the second, even after various attempts to make it more salient.

3.2. Non-guided sequences: 2 targets in a set of 3 (2T+1D)

3.2.1. Search for the sequence

Fig. 2A shows the evolution of the average number of trials to find a sequence (parameter N) during the 24

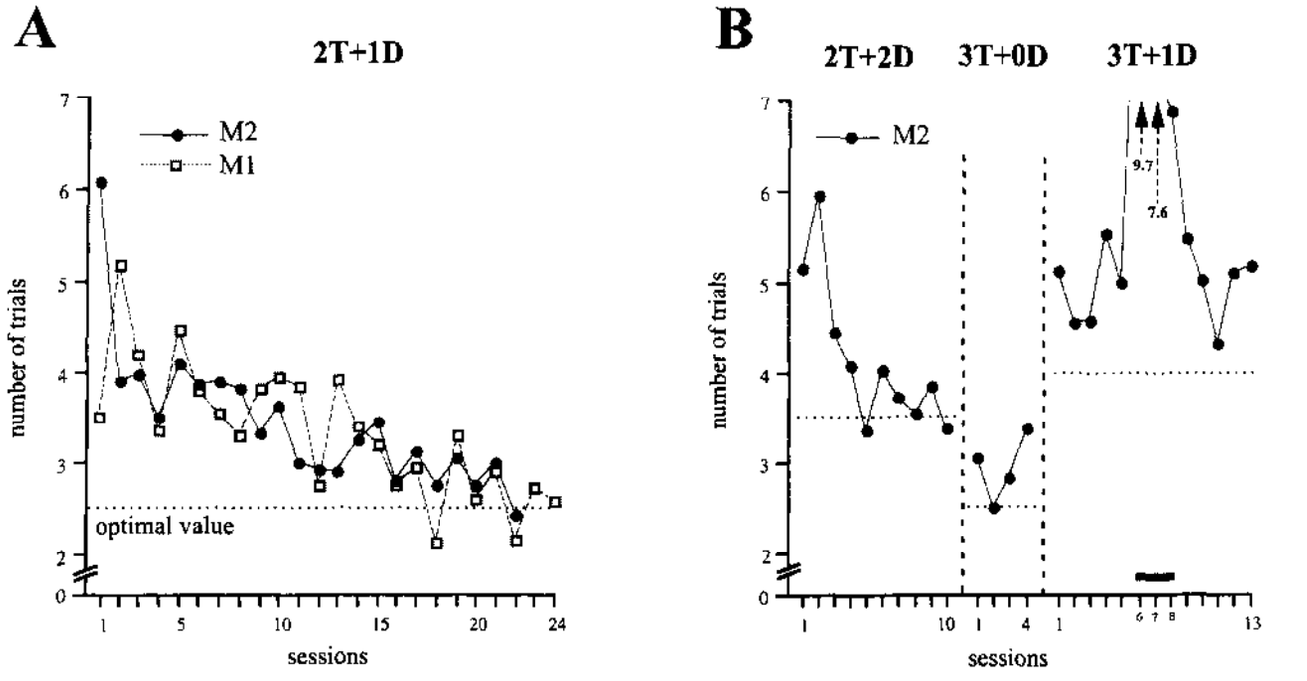


Fig. 2. Average number of trials to discover a sequence. In A, monkeys 1 and 2 (M1 and M2) in the search for 2 targets in a set of 3 (2T+1D) during 24 successive sessions. In B, monkey 2 in the search for, successively, 2 targets in a set of 4 (2T+2D), 3 targets in a set of 3 (3T+0D), and 3 targets in a set of 4 (3T+1D). Dotted lines indicate the optimal average number in the corresponding task. The large thick line above the abscissa in B indicates 3 training sessions (6–8) in which the task (3T+1D) was different (V2; see Materials and methods). In A, the animals approach optimal performance. The improvement between the 6 first and 6 last training sessions is statistically significant (t-test) (M1, $t=6.02$, $P<0.0001$; M2, $t=3.98$, $P<0.0001$). In B, the deviations from the optimal N are statistically different in the 2T+2D and 3T+1D tasks (t-test on the last 5 sessions) ($t=3.67$, $P<0.01$). This indicates that the search for a sequence of 3 items is not only longer, but also more difficult than for a sequence of 2.

first training sessions in the two monkeys. It decreased towards its optimal value (2.5); it reached 2.94 and 2.79 during the last 5 sessions in monkeys 1 and 2, respectively. During the last session, monkey 1 found the sequences, on the average, in 2.57 trials. These results show that the monkeys become more and more efficient in the search process.

The improvement is due to different factors: (1) by the end of the training period, an error was almost never repeated. For instance, in the second training session, 29% of the errors in monkey 1 and 17% in monkey 2 were a repetition of a previous error; during the last session, these percentages dropped to 5 and 9% respectively; and (2) Probability P increased all along the training session (Fig. 3A).

Monkey 1 had partially understood that two successive different sequences never started with the same first target. For the 7 last training sessions, Fig. 4A shows the frequency with which each target was chosen as first target in the first trial of a new sequence, according to the position of the first target in the preceding sequence. Target Right (respectively Left) was chosen more often when the preceding first target was target Left (respectively Right). This explains that the average number of trials to find the solution dropped in some sessions below the optimal value 2.5 and remained close to 2.0, which is the optimal N if the rule concerning the first targets of two successive sequences is taken into account (Fig. 2A).

Monkey 2 had a stereotyped search. Apparently, he did not notice that two successive sequences never had the same first target. He frequently started the search for a new sequence with a hit of the upper target (Fig. 4B). If the upper target was not the good one, then he hit the left one and lastly the right one (in this order). When the first target was found, then the animal invariably chose as the second target, whenever it was possible, a target that had not been hit erroneously as the first target in the preceding trial.

3.2.2. *Consolidation of the correct response*

Fig. 5A shows that the number of errors during the consolidation period decreased over the course of subsequent training sessions. Evolution of this parameter is comparable to the evolution of N in Fig. 2A. Monkey 2 consistently lost the sequences much more frequently than monkey 1. During the last 5 training sessions, the mean number of errors was 0.41 for monkey 1 and 0.86 for monkey 2.

3.2.3. *Time interval between lever onset and monkey's lever touch (LT)*

We have selected in the last 5 training sessions of M1 and M2 all the sequences in which, after discovery of the correct response, the animal correctly performed 5 correct responses in a row, without error. In this group, two sub-groups were considered according to the number of trials preceding the first correct sequence (Fig. 6). In the two upper diagrams, the correct sequences (C) are preceded by 1 incorrect trial (1C) (in abscissa); in the lower diagrams, the correct sequences by 2 incorrect trials. In monkey 1, parameter LT is significantly

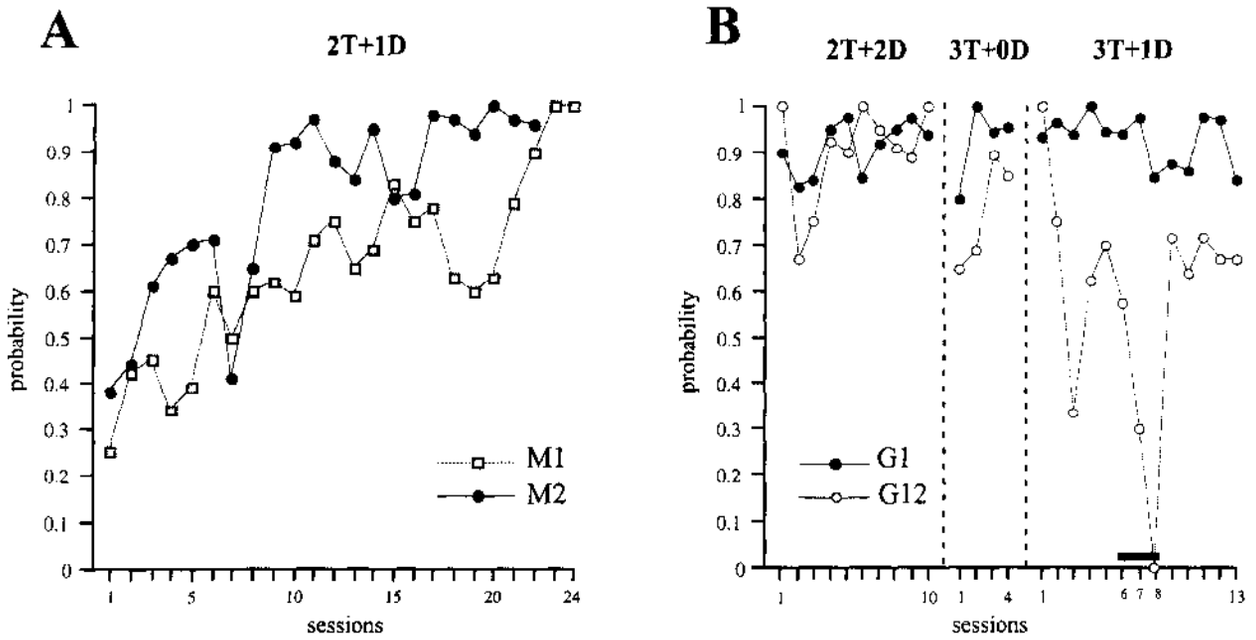


Fig. 3. Probability of keeping the first (correct) target in the trial which follows its discovery. Comparison of the two monkeys and of different tasks (see Fig. 2 for abbreviations). In A, the probability is close to 1.0 in the last training sessions in the two monkeys. In B, probability sub-group G1 is close to 1.0 in all tasks. G1 and G12 are statistically different in the 3T + 1D task (t-test) ($t = 3.58$, $P < 0.001$), but not in 2T + 2D task ($t = 0.01$, NS). This indicates that memorising 3 spatial items acquired at the same time is more difficult than memorising 2.

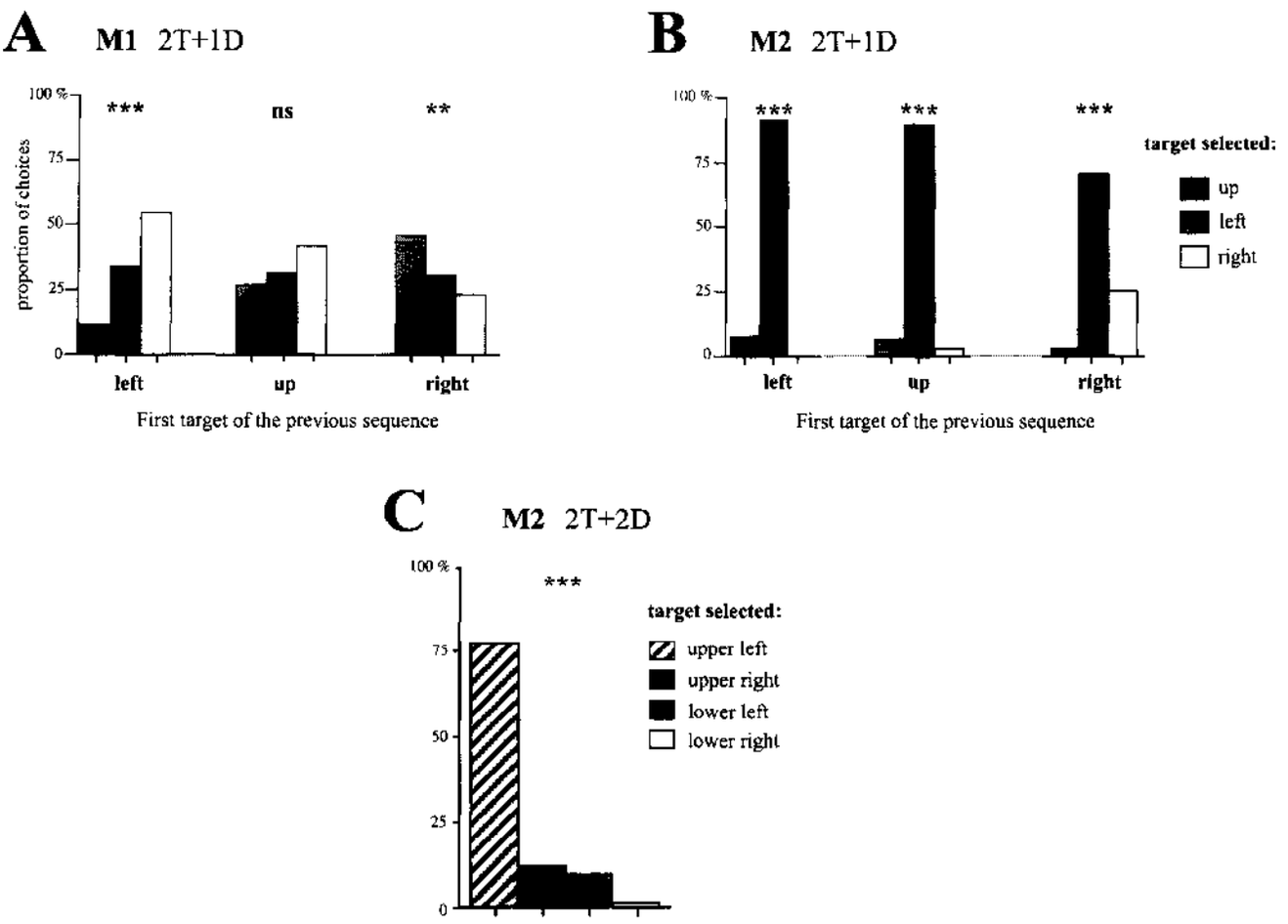


Fig. 4. First choice in a new search. A: monkey M1 in the 2T+1D task. B: monkey M2 in the 2T+1D task. C: monkey M2 in the 2T+2D task. Choice (during the 7 last training sessions) of the different targets in the first trial of a new search (frequency in ordinate), according to the position of the first target of the preceding sequence (in abscissa). In A, the choices depend on the previous sequence (χ^2 one-sample test). From left to right: $\chi^2(df=2)=28.30$, $^{***}P<0.001$; $\chi^2(df=2)=3.89$ non-significant (NS); $\chi^2(df=2)=8.37$ $^{**}P<0.02$. In B and C, the choices do not depend on the previous sequence. From left to right in B: $\chi^2(df=2)=158.97$, $P<0.001$; $\chi^2(df=2)=147.78$, $P<0.001$; $\chi^2(df=2)=73.64$, $P<0.001$. In C, $\chi^2(df=3)=149.72$, $P<0.001$.

smaller in the trial (indicated by an arrow) following the first success. This indicates that monkey 1 showed a specific haste to start a trial after the first success. The result is consistent with the good consolidation of the correct response observed in this animal. In monkey 2, LT is significantly smaller during the search process. This indicates that the animal had a specific haste to use, at each stage of the search process, but not beyond (i.e., during the consolidation), partial knowledge acquired about the correct solution. The result is consistent with the good construction of the solution (Fig. 3), but relatively poor consolidation (Fig. 5).

3.2.4. Eye movements

Fig. 7I and II show representative examples in monkeys 1 and 2 of the oculomotor activity between the beginning of the central fixation and 2 s after the last press all along the search and consolidation of a sequence 'Up-Right'. Monkey 1 did not use the 800 ms after extinction of the FP, in which oculomotor activity was free, to explore the target display. He directed his gaze directly from FP to the selected target (7I, 1 and 2). After a correct hit, he also directed his gaze directly towards the next target (7I, 2). Monkey 2 explored the display a little more during the search period (7II, 1, 2 and 3). During the consolidation, he did not explore the display (7II, 4). These data suggest that, at most stages of the search and consolidation periods, selection of the target to press is made during fixation of the preceding target, or even before.

The direction of spontaneous eye movements following an incorrect press was not indicative of the targets that the animal selected in the next trial. Analysis in monkey 1 of the oculomotor activity following 30 erroneous presses of the first target shows that, in 9 trials, the animal oriented towards a target position (the upper target in 7I, 1) and pressed the corresponding target at the first rank in the next trial (7I, 2); in 9 other

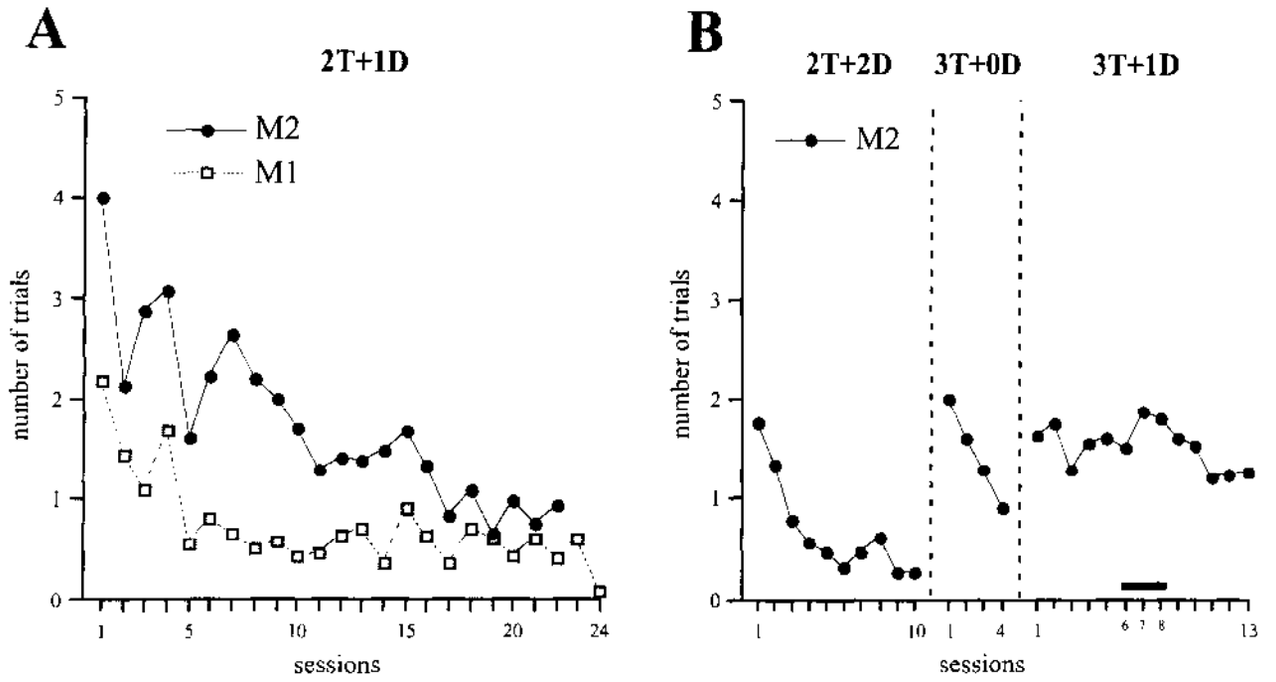


Fig. 5. Evolution of the number of errors during the consolidation period. Comparison of the two monkeys and of different tasks (see Fig. 2 for abbreviations). In A, the animals improve the memorisation of the sequences during the course of the training sessions. The improvement between the 6 first and the 6 last training sessions is statistically significant (t-test) (M1, $t=5.21$, $P<0.0001$; M2, $t=14.92$, $P<0.0001$). In B, the number of errors during consolidation is statistically different in the 2T+2D and 3T+1D tasks (t-test on the last 5 sessions; $t=10.32$, $P<0.0001$).

trials, he oriented towards a target position, but pressed another target in the next trial, and in 10 trials, his oculomotor activity showed no apparent purpose. Analysis of the oculomotor activity during the 2 s following 21 errors in monkey 2 gave similar results. These data suggest that correcting the plan after an error is an internal process without immediate and overt expression in terms of oculomotor activity.

3.3. *Non-guided sequences: 2 or 3 targets in a set of 4*

3.3.1. *Search for the sequence*

Fig. 2B shows the evolution of parameter N in the different tasks performed by monkey 2 with 4 targets. Although the search process was longer in the 2T+2D task than in the 2T+1D task (optimal N is 3.5 and 2.5, respectively), deviation of N with respect of these optimal values was statistically the same in both tasks (t-test) ($t=0.49$). The same results appeared in the 3T+0D task. These data indicate that increasing the complexity of the environment (4 targets instead of 3) made the search longer but did not increase the number of error repetitions or failures to consolidate successful touches. In other words, searching a sequence of 2 targets in a set of 3 or 4 targets seems to represent the same difficulty for the working memory.

The training in the 3T+1D task was sub-divided into 3 periods. In the first period (sessions 1–5), version V1 of the task was used; in the second (sessions 6–8, indicated by a thick horizontal line above the axis of abscissa on Fig. 2B), the animal worked with V2. The figure shows that, with V2, the scores of the animal deteriorated. The animal very often hit as third target, the (already hit) first target of the sequence. He had not understood that a target could only be hit once in a sequence. As a consequence, part of the sequence already constructed by the animal was lost. Little by little, the animal refused to work. In the last period (sessions 9–13), the animal worked with V1 again. The results obtained in the first and third periods show that the search of a sequence of 3 targets not only required more time than a sequence of 2 (2D+2D) (optimal N was 4), but that the deviation from the optimal value was larger. This indicates that repetitions of errors or the forgetting of successes occurred more frequently. Clearly, construction, storage and/or recall of a sequence of 3 targets, even in the simplified condition V1, represented a more difficult task than storage and/or recall of a sequence of 2 targets.

Fig. 3B shows the values of probability P of keeping the first correct target in the trial which follows its discovery,in the 2T+2D, 3T+0D and 3T+1D tasks. Probability P was compared in two groups of trials. In one group (G1), P is calculated in all trials following acquisition of the first target only (the monkey had to memorise two temporospatial items: the positions of the first correct and of the second incorrect targets). Probability P is not statistically different in the 2T+2D, 3T+0D and 3T+1D tasks. In another group (G12), P was calculated in all trials following acquisition of the

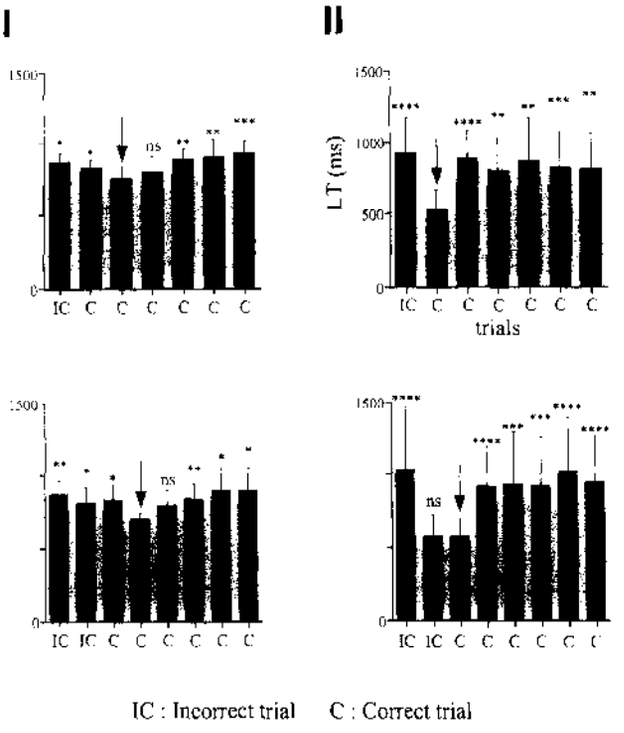


Fig. 6. Average time intervals (LT) between lever onset and lever touch during search and consolidation in the 7 last training sessions in the 2T+1D Task. Data are given for monkey 1 (I) and monkey 2 (II). In I, the number of sequences is $n=9$ and $n=7$ in the upper and lower diagrams. LT in the trial (indicated by an arrow) which follows the discovery of the sequence is shorter than in the other trials (t-test) ($0.90<t<4.03$). In II, the number of sequences is $n=17$ and $n=25$ in the upper and lower diagrams. LT is shorter during the search process (t-test) ($0.15<t<7.45$; NS, $^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$, $^{****}P<0.0001$).

first *and* second targets in the same trial (In the 2T+2D task, the animal had to memorise the positions of the 2 correct targets; in the 3T+1D task, the animal had to memorise the 2 correct targets and the position of the incorrect target hit at the third rank). In the 2T+2D task, P is not different in G1 and G12, i.e., whether the animal had to memorise the positions of two correct items or of one correct and one incorrect. In the 3T+1D task, acquisition of 3 temporospatial items in a single trial had a disrupting effect on parameter P.

Monkey 2 almost always started the search of a new sequence with the hit of the upper-left target (Fig. 4C); if the first correct target was not the upper left, his next choice as first target was less predictable.

3.3.2. *Consolidation of the correct response*

Fig. 5B shows the evolution of the average number of sequence losses after the first sequence discovery. Comparison of the scores obtained in the 2T+2D and the 2T+1D tasks confirms that increasing the number of distractors by 1 does not make consolidation more difficult. Indeed, the results even suggest that the 2T+2D consolidation was significantly better ($t=4.77$, $P<0.005$)

The results also show that good consolidation of successful sequences is more frequent in the 2T+2D than in the 3T+1D task (at $P<0.0001$). These results are in agreement with the results of the search process. In the 3T+1D task, two-thirds of the errors during consolidation occurred after the first or the second successes, i.e., at the beginning of the consolidation period; 20% of the sequence losses occurred at the end of the period, after the fourth and fifth successes. Two errors were responsible for 70% of the failures: when the monkey has to repeat the sequence ABC (A, B and C indicating any one of the 4 targets), he often performs AC (skipping B) or pressed B first (skipping A).

3.3.3. *Eye movements*

Fig. 8 shows representative examples of the oculomotor activity of monkey 2 during search and consolidation of a sequence 'lower-Left, upper-left' in the 2T+2D task. The animal found the solution in 4 trials and performed the 5 repetitions in a row without errors.

In Fig. 8A, the animal worked 'gaze-free' (it fixated the central FP when it was illuminated; when FP was extinguished, gaze was free). The exploratory activity was dense during the search period (Fig. 8A-1–3). During the consolidation period (Fig. 8A-4), it remained dense although the monkey knew the solution. We did not observe preferential saccades between the two targets of the sequence. In Fig. 8A-4 even, most saccades link the upper-left target to the lower-right target which does not belong to the sequence. Attention was distributed over the 4 targets. Indeed, during consolidation of 15 sequences in the (2T+2D) task, 31% of the time spent in target fixations, between offset of the FP and the second touch, was devoted to the two targets which did not belong to the sequence. In Fig. 8B (5 months later), the animal worked with the fixation condition. He still continued to scan the display during the search period (Fig. 8B-1–3). During the consolidation period, oculomotor activity until the touch of the second target was restricted to the trajectory FP–first target–second target.

4. Discussion

The above data show that normal macaque monkeys can be conditioned to perform a spatial problem-solving task. This is, in itself, an important result. The good performance results from a search strategy, i.e., from an implicit spatial reasoning. The reasoning is logical since it reflects the logic of action (get the reward as fast as possible). It has direct relationships with practical (success) or presymbolic intelligence. The reasoning, and the mental operations that are associated with it, originate from the sensorimotor activities of the animal, from its capacity to store spatiotemporal data and to reflect upon them.

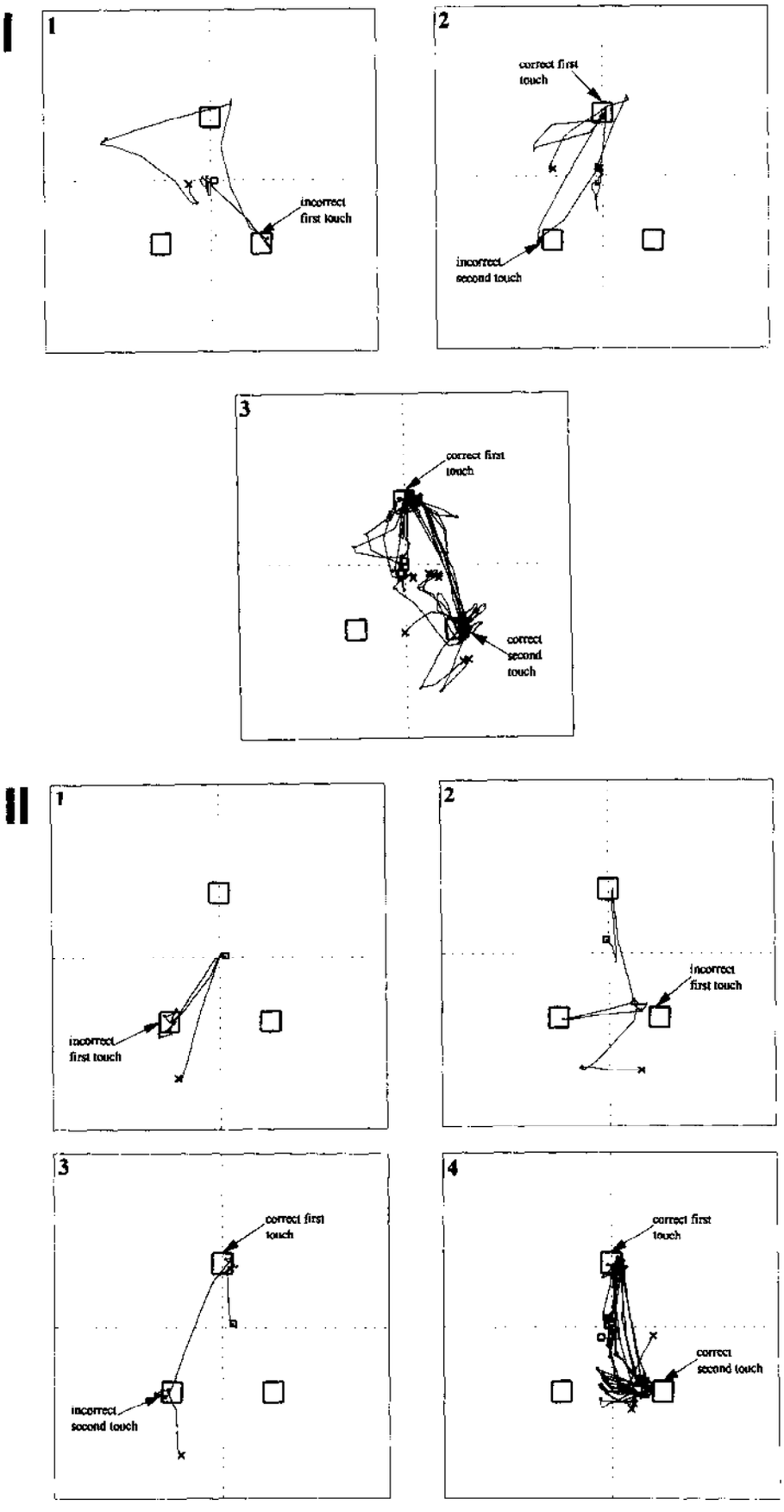


Fig. 7. Oculomotor activity during search and repetition of the sequence up-right in the 2T + 1D task in monkey 1 (I) and in monkey 2 (II), between the beginning of the central fixation (□) and 2 s after the last press (×). In I, monkey 1 pressed the right target (1), the upper and the left targets (2). In 3, it performs 6 correct sequences in a row. In II, monkey 2 pressed the left target (1), the right target (2), the upper and the left targets (3). In 4, it performs 6 correct sequences in a row.

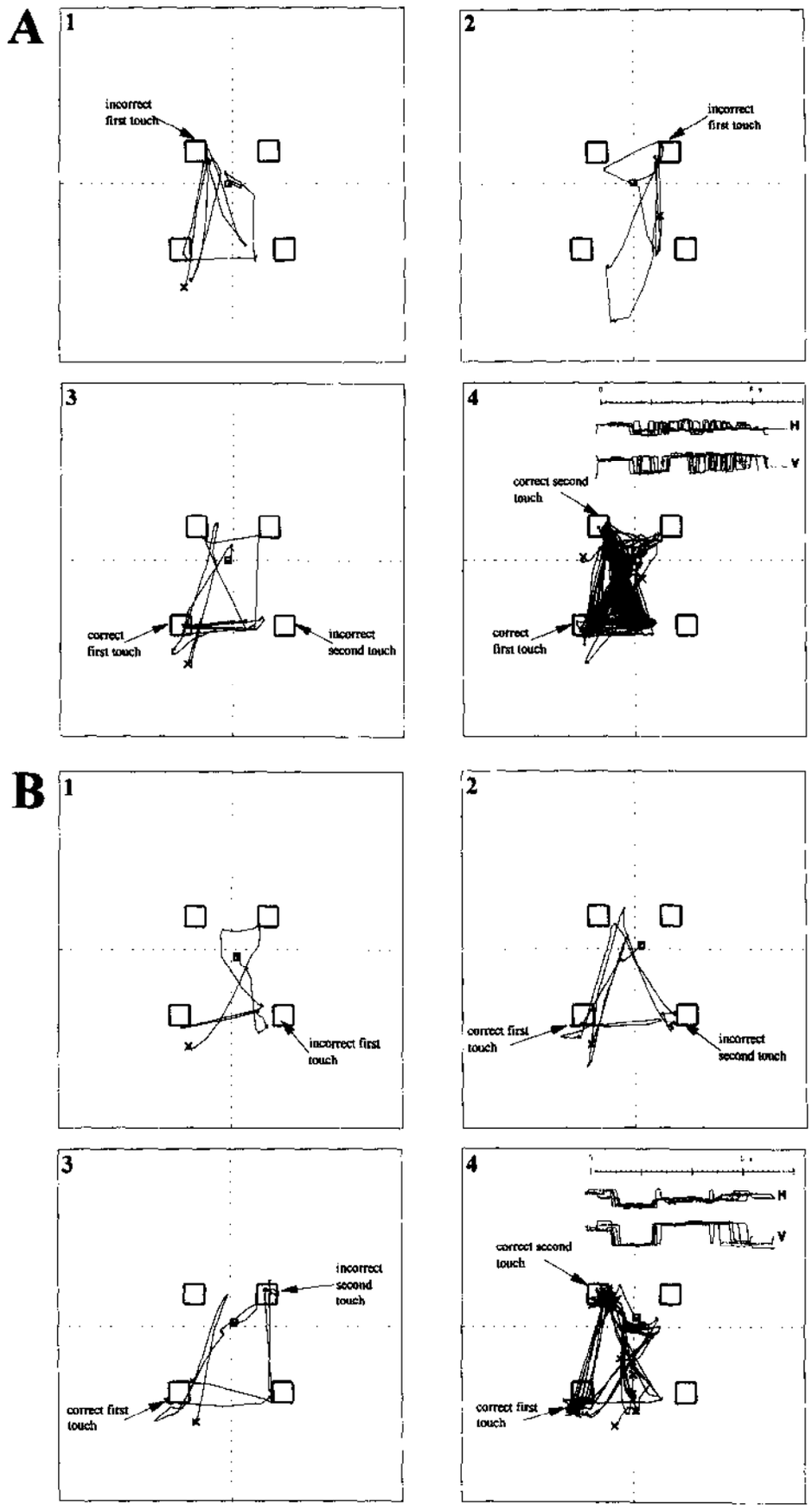


Fig. 8. Oculomotor activity during search and repetition of the sequence 'lower-left, upper-left' in the 2T + 2D task in monkey 2 without (A) and with (B) the fixation task, between the beginning of the central fixation (□) and 2 s after the last press (×). In A, the animal pressed the upper-left target (1), the upper-right target (2), the lower-left and the lower-right targets (3). In 4, it performs 6 correct sequences in a row. In B, it pressed the lower-right target (1), the lower-left and the lower-right targets (2), the lower-left and the upper-right targets (3). In 4, it performs 6 correct sequences in a row.

In monkey 1, after exposure to the non-guided version of the 2T+1D task and acquisition of an optimal strategy, we observed a drop in the performance of the 2T+1D guided task. The animal seemed to pay less attention to the location of the second target during the instruction period. Monkey 2 never learned the guided task correctly. In contrast, he performed different versions of the non-guided task well. These data are compatible with the hypothesis that the non-guided task is easier for the animals, at least when the total number of targets is small. A possible explanation is that, although the memory load is the same for the two tasks, acquisition of complex spatiotemporal information directly provided by the environment in a short delay period (the guided task) is more demanding in terms of attention and/or requires other memory registers than acquisition of the same information by trial-and-error through the motor activity of the subject over a longer period (the non-guided task). The non-guided task is also partly based on spontaneous alternation, a behaviour which is observed in other animals such as the mouse [3], and to which evolution has probably given a strong neural substrate.

Analysis of performance shows that the search for the first target was conducted in a minimum number of trials; each error was taken into account and was used to modify the successive choices. Repetition of an error appears as a transient lack of attention. After 24 training sessions in monkey 1 and 9 in monkey 2, once the animal had found the first target in a set of 3, he kept it in the next trial (Fig. 3A). If the first target was found, but the second was incorrect, the animal kept the first, but changed the second. The first target was understood as part of the correct response. Thus, the animal maintained part of his response and, independently, modified the other part. As a consequence, he constructed the solution step-by-step, by an integration of the location and rank of the successful and erroneous target touches. The strategy of keeping part of the correct response and of changing the incorrect part was also used by monkey 2 when he had to find 3 targets in a set of 4 (Fig. 3B). These results confirm that monkeys can construct complex cognitive structures to solve spatial problems.

Our results underline some obvious functional characteristics of spatiotemporal working memory in monkey. A sequence of 2 items is easier to memorise than a sequence of 3; memorising a sequence of 2 or 3 items acquired at the same time is more difficult than memorising the same number of items acquired at different times. The animals reduce the duration of the inter-trial period at selected stages of task to optimise the attentional factors attached to performance of the working memory.

Before being trained on the fixation condition, the animals showed a very dense oculomotor activity during the trials (Fig. 8A), which is reminiscent of the dense and apparently erratic exploration observed in many mammals placed in a novel environment [17]. With the fixation task, they strongly reduced their oculomotor scanning of the target display, in particular during the consolidation period. They worked less, but reached the same levels of performance as when 'head-free'. Thus, part of the oculomotor activity observed in the situation 'gaze-free' is not necessary for the setting-up and execution of the sequence plan. It might, nevertheless, have a functional role.

One hypothesis is that oculomotor scanning of the target display diminishes the attentional load of the task. For instance, intermittent fixation of a visual target could alleviate the attention to the 'GO' signal delivered by the target and/or to preparation of an arm movement towards this target. Oculomotor scanning of the target display could also maintain the plan in a state of accessibility which reduces the use of the spatial working memory and of the attentional processes that are attached to it. It would give frequent access to the targets and to memory of their behavioural value. It has been shown that human subjects, in natural tasks, seek to minimise the use of short-term memory and use alternative strategies if their cost is lower [1]. When the monkey worked head-free and after an erroneous target-press, we often observed in the next trial that he seemed to reproduce the same press at the same rank. He began the same arm movement, but halted and directed his gaze and his arm towards another target. An explanation of this behaviour is that fixation of the target and the arm-movement preparation had automatically (i.e., regardless of attentional processes, and thus at lower cost) recalled the memory of the detrimental consequence of the corresponding movement made in the previous trial; hence, the orientation towards another target. Another hypothesis is that spontaneous ocular scanning of the target display facilitates formation, storage and recall of the oculomotor plan. Unit recordings in prefrontal cortex have shown that the neuronal representation of a spatial plan depends on the direction of gaze [2]. Thus, a dense oculomotor scanning of the target display, i.e., different directions of gaze, may reinforce the central representation of the sequence by creating and permanently recalling different neuronal versions of this sequence.

The search for sequences within the physically invariant elements of a stable spatial context requires constant and rapid flexibility in the plans developed by the animal. In this respect, the task has some similarities with the Wisconsin Card Sorting Test (WCST) [9] used in patients although, unlike the WCST, its execution requires acquisition and execution of a learning set. It also has many links with the 'visual stepping-stone' maze test [10] the self-ordered pointing task [13] and the Tower of London test [16]. Lesions studies [11,13] and PET studies [5,15] have shown the involvement of the prefrontal cortex in these tasks.

Monkeys with lesions of the prefrontal cortex are impaired in self-ordered tasks which require organizing sequences of responses or choices [4,12,14]. This deficit has been related to an impairment in monitoring information within working memory and in the development or use of motor strategies. Our hypothesis is that the prefrontal cortex is also specifically involved in the present task. Previous results suggest that at least some of the relevant neuronal populations may be located in and around area 8 [2].

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References

[1] Ballard, D.H., Hayhoe, M.M. and Pelz, J.B., Memory representations in natural tasks, *J. Cognitive Neurosci.*, 7 (1995) 66–80.

[2] Barone, P. and Joseph, J.P., Prefrontal cortex and spatial sequencing in macaque monkey, *Exp. Brain Res.*, 78 (1989) 447–464.

[3] Beracochea, D., Lescaudron, L., Tako, A., Verna, A. and Jaffard, R., Build-up and release from proactive inference during chronic ethanol consumption in mice: a behavioral and neuroanatomical study, *Behav. Brain Res.*, 25 (1987) 63–74.

[4] Collins, P., Everitt, B.J., Robbins, T.W. and Roberts A.C., A novel test of spatial working memory in primates: contrasting effects of excitotoxic lesions and dopamine depletion of the prefrontal cortex in the marmoset, *Soc. Neurosci. Abstr.*, 21 (1995) 566.23.

[5] Frith, C., Positon emission tomography studies of frontal lobe function: relevance to psychiatric disease. In: *Exploring Brain Functional Anatomy with Positon Tomography. Ciba Foundation Symposium 163*, Wiley, Chichester, 1991, 181–197.

[6] Fuster, J.M., *The Prefrontal Cortex. Anatomy, Physiology, and Neuropsychology of the Frontal Lobe*, Raven press, New York, 1989.

[7] Goldman-Rakic, P.S., Circuitry of primate prefrontal cortex and regulation of the behavior by representational memory. In: *Handbook of Physiology. The Nervous System. Higher Functions of the Brain, Vol. 5*, Am. Physiol. Soc., Bethesda, 1987, pp. 373–417.

[8] Kermadi, I. and Joseph, J.P., Activity in the caudate nucleus of monkey during spatial sequencing, *J. Neurophysiol.*, 74(3) (1995) 911–933.

[9] Milner, B., Effects of different brain lesions on card sorting, *Arch. Neurol.*, 9 (1963) 90–100.

[10] Milner, B., Visually-guided maze learning in man: effects of bilateral hippocampal, bilateral frontal, and unilateral cerebral lesions, *Neuropsychologia*, 3 (1965) 317–338.

[11] Owen, A.M., Downes, J.J., Sahakian, B.J., Polkey, C.E. and Robbins, T.W., Planning and spatial working memory following frontal lobe lesions in man, *Neuropsychologia*, 28(10) (1990) 1021–1034.

[12] Passingham, R.E., Memory of monkeys (Macaca mulatta) with lesions in prefrontal cortex, *Behav. Neurosci.*, 99(1) (1985) 3–21.

[13] Petrides, M. and Milner, B., Deficits on subject-ordered tasks after frontal- and temporal-lobe lesions in man, *Neuropsychologia*, 20 (1982) 249–262.

[14] Petrides, M., Impairments on nonspatial self-ordered and externally ordered working memory tasks after lesions of the mid-dorsal part of the lateral frontal cortex in the monkey, *J. Neurosci.*, 15(1) (1995) 359–375.

[15] Petrides, M., Alivisatos, B., Evans, A.C. and Meyer, E., Dissociation of human mid-dorsolateral from posterior dorsolateral frontal cortex in memory processing, *Proc. Natl. Acad. Sci. USA*, 90 (1993) 873–877.

[16] Shallice, T., Specific impairments in planning, *Phil. Trans. R. Soc. Lond. B*, 298 (1982) 199–209.

[17] Thinus-Blanc, C., Animal spatial cognition. In: L. Weiskrantz (Ed.), *Thought Without Language. Third Fyssen Symposium*, Oxford University Press, 1988, pp. 371–395.