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Spatial reasoning in the monkey

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1. Introduction

Rhesus monkeys (*Macaca mulatta*) are able to memorise the order of illumination of three fixed spatial targets and, after a delay, to press them in the same order [1,4]). This working memory task entails complex neuronal processes such as the capacity to integrate the spatio-temporal information given by the environment (the order in which the targets were illuminated) into a spatial plan, to store it and later, during the target-press phase, to update the plan as it is executed, according to the location of the targets that have been already pressed.

In the present study we analysed the behavioural data obtained in two rhesus monkeys in a problem-solving situation derived from the spatial task described above. The task consisted of finding, by trial-and-error, the correct order of touching two or three targets in a set of three or four fixed spatial targets.

2. Experimental procedures

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

In one series of experiments, the animal worked with three targets. One was located 7.5 cm above the centre of the screen (target U); two lower targets were located 7.5 cm to the right (target R) and to the left (target L) and 7.5 cm below the centre. In another series of experiments, four targets were used (Fig. 1). Two upper targets were located 5.5 cm to the right and to the left and 4 cm above the centre; two lower targets were located 7.5 cm to the right (target R) and to the left (target L) and 7.5 cm below the centre. In both series, a 3 × 3 cm white square, located 10 cm below the centre, served as starting lever. The PC recorded touches and visual events on the same time scale.

The monkey had to discover, by trial-and-error, the pressing order of two or three targets. To start a trial (Fig. 1), 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 this instruction period, all targets were simultaneously illuminated at times 500 for 500 ms. At the end of the instruction, all three targets were simultaneously illuminated "grey" during 1.5 s. When their colour turned "white" (white period = "go" signal), the animal had to release the lever and touch the target that it had chosen to hit first. If the touch was correct, all three 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. If there was a third target to press, the targets turned white again and the animal had to touch the third target. Each correct touch was signalled by a short tone delivered to the animal from a buzzer located above the screen. The correct trials were rewarded; the incorrect trials were aborted and the research process was resumed from the beginning until it was successful. A time interval of 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 two targets in a set of two. When the task was mastered, they were tested in the search for two targets in

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a set of three (two targets and one distractor = 2T + 1D). One monkey (monkey 2) was then trained and tested in the search for two targets in a set of four (2T + 2D) and for three targets in a set of three (3T + 0D). When it mastered these tasks, it was tested in the search for three targets in a set of four (3T + 1D) (Fig. 1). In this last task, two versions were administered to the animal. In one version (V1), after the second target of the sequence had been found, only the two 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 experimentally restricted to the two remaining non-pressed targets. In the second version (V2), all targets turned bright for the third hit.

Each sequence was repeated until the animal had performed a total of six correct trials. This repetition was aimed at studying the consolidation processes following the discovery of the correct order. When the series of six correct trials was terminated, a central red circle was flashed several times on the screen and a tone was delivered through the loudspeaker, 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 six different sequences of two targets in the set of three targets, 12 sequences of two targets and 24 sequences of three targets in the set of four. In each training session –which lasted approximately 2–3 h – the monkey initialised up to 60 searches.

Two periods were analysed: the search and the consolidation of the correct sequence. During the search period, two parameters were retained: (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 case of the search for two targets in a set of four, the solution can be found between one (at best) and six (at worst) trials; thus, optimal N was 3.5. Optimal N in the different tasks is indicated in Fig. 2A and C. (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 improvement in 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.

3. Results

3.1. Search for two targets in a set of three (2T + 1D)

3.1.1. Search for the sequences

Fig. 2A shows the evolution of parameter N during the 24 first training sessions in the two monkeys. Parameter N decreased towards its optimal value (2.5). N had an average value of 2.94 and 2.79 during the last five sessions in monkeys 1 and 2 respectively. During the last session, monkey 1 found the sequences, on 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. (2) The probability P increased in the two monkeys all along the training sessions (Fig. 2B).

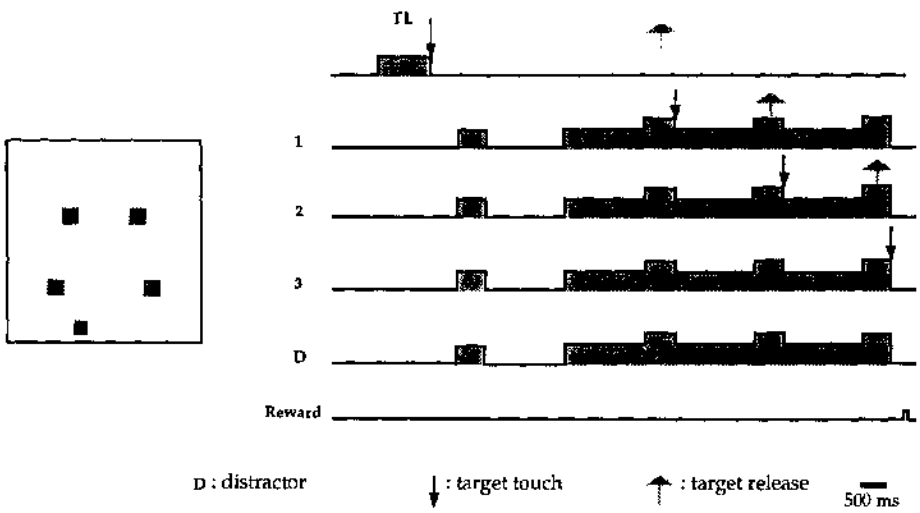


Fig. 1. Behavioural paradigm. Schematic representation of the set-up with four targets. Definition of the events: 1, 2, 3, notations indicating the pressing order of the targets. Grey area, time of illumination of the targets; higher amplitude in the grey area, full illumination (GO signal). See Section 2 for details.

3.1.2. Consolidation of the correct response

Fig. 3A 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 sequence much more frequently than

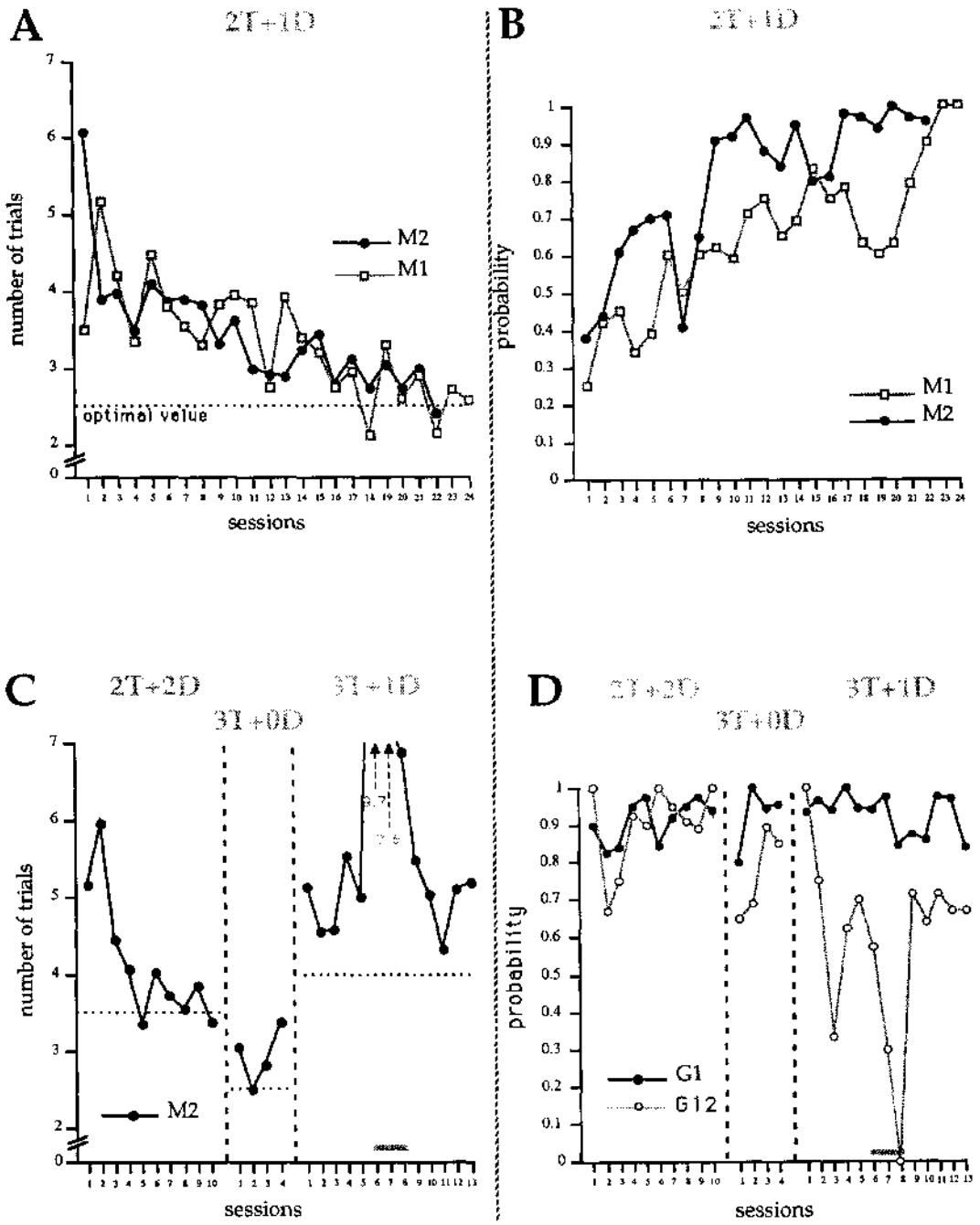


Fig. 2. A and C: average number of trials to discover a sequence. In A, monkeys 1 and 2 (M1 and M2) in the search for two targets in a set of three (2T + 1D) during 24 successive sessions. In C, monkey 2 in the search for, successively, two targets in a set of four (2T + 2D), three targets in a set of three (3T + 0D), and three targets in a set of four (3T + 1D). Dotted lines indicate the optimal average number of trials in the corresponding task. The large line above the abscissa in C indicates three training sessions (6, 7, 8) in which the task (3T + 1D) was different (V2, see Procedures). In A, the animals approach optimal performance. The improvement between the six first and six last training sessions is statistically significant (t test; M1: $t = 6.02$, $P < 0.0001$, and M2: $t = 3.98$, $P < 0.0001$). In C, the deviations from the optimal N are statistically different in the 2T + 2D and 3T + 1D tasks (t test on the last five sessions; $t = 3.67$, $P < 0.01$). This indicates that the search for a sequence of three items is not only longer, but also more difficult than a sequence of two. B and D: probability (P) of keeping the first (correct) target in the trial which follows its discovery. Comparison of the two monkeys and of different tasks. In B, P is close to 1.0 in the last training sessions in the two monkeys. In D, P of sub-group G1 is close to 1.0 in all tasks. G1 and G12 are statistically different in the 3T + 1D task (t test; $t = 3.58$; $P < 0.001$). There is no difference in the 2T + 2D task ($t = 0.01$, ns). This indicates that memorising three items acquired at the same time is more difficult than memorising two.

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. Search for two or three targets in a set of four

3.2.1. Search for the sequences

Fig. 2C shows the evolution of parameter N in the different tasks performed by monkey 2. Although the search process was longer in the 2T + 2D task than in the 2T + 1D task (optimal N was 3.5), the deviations of the actual scores from the optimal values were statistically the same in both tasks (t test; $t = 0.49$). They were also the same in the 3T + 0D task. These data indicate that increasing the complexity of the environment (four targets instead of three) made the search longer but did not increase the number of error repetitions or failures to consolidate successful sequences. In other words, searching for a sequence of two targets in a set of three or four targets represents the same difficulty for the working memory.

The training in the 3T + 1D task was sub-divided into three periods. In the first period (sessions 1–5), version V1 of the task was used; in the second (sessions 6, 7 and 8, indicated by a thick horizontal line above the axis of the abscissa in 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. It 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 since it did not understand at that point that a given target could be correct at the first rank and erroneous at the third. 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 three targets not only required more time than a sequence of two (2T + 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 three targets, even in the simplified condition V1, represented a more difficult task than storage and/or recall of a sequence of two targets.

Fig. 2D shows the values of probability P in the 2T + 2D, 3T + 0D and 3T + 1D tasks. P was compared in two groups of trials. In one group (G1), P was calculated in all trials following acquisition of the first target only; the monkey had to keep in memory two temporo-spatial items, the positions of the first (correct) and of the second (incorrect) targets, hit respectively at the first and second rank. 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 the acquisition of the first and second targets in the same trial. In the 2T + 2D task, the animal had to keep in memory the positions of the two first correct trials; in the 3T + 1D task, it had to keep in memory these positions and the position of the (incorrect) third target hit at the third rank. In the 2T + 2D task, the data show that P is not different in G1 and G12, i.e., whether the animal had to keep in memory the positions of two correct items or of one correct and one incorrect. In the 3T + 1D task, the data show that acquisition of three temporo-spatial items in a single trial had a disrupting effect on parameter P.

3.2.2. Consolidation of the correct response

Fig. 3B shows the evolution of the average number of sequence losses after the first sequence discovery. Compar-

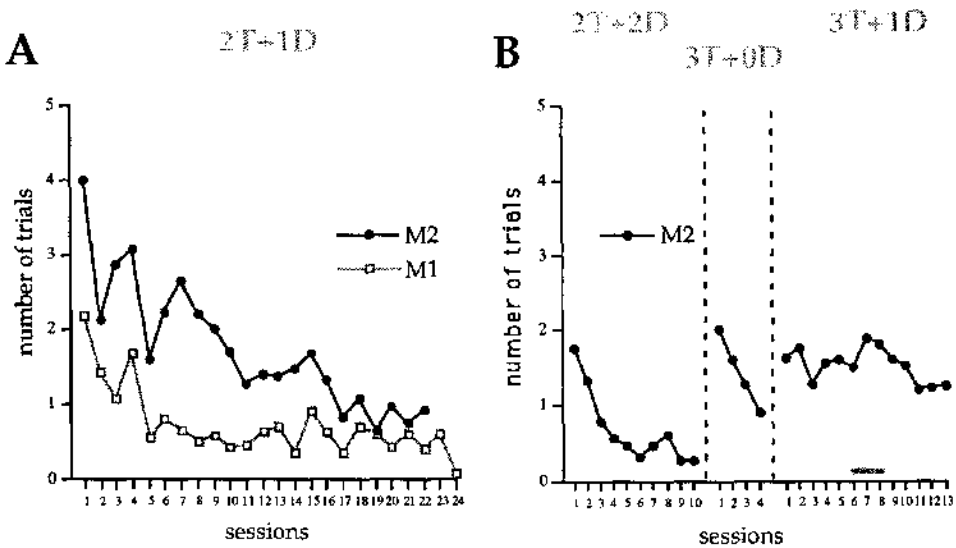


Fig. 3. Evolution of the number of errors during the consolidation period. Comparison of the two monkeys and of different tasks (see Fig. 2 for abbreviations). In A, the animals improve the memorisation of the sequences during the course of the training sessions. The improvement between the six first and the six last training sessions is statistically significant (t test; M1: $t = 5.21$, $P < 0.0001$, and 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 five last sessions; $t = 10.32$; $P < 0.0001$).

ison 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.

4. Discussion

Analysis of performance in the 2T + 1D task shows that, during the last training sessions, 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. Rare 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 three, it kept it in the next trial (Fig. 2B). 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 its response and, independently, modified the other part. As a consequence, it 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 it had to find three targets in a set of four (Fig. 2D).

These results confirm that monkeys can construct complex cognitive structures to solve spatial problems. The good performance results from an adapted search strategy, i.e., from a spatial reasoning. The reasoning and the mental operations that are associated with it originate from the sensorimotor activities of the animal, from its capacity to store spatio-temporal data and to reflect upon them. The reasoning is logical since it reflects the logic of action (get the reward as fast as possible). It has a direct relationship with practical (success) or pre-symbolic intelligence.

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) although, unlike the WCST, its execution requires acquisition and execution of a learning set. The task has also many links with the spatial delayed response in monkey (see [3] and [2] for reviews), with the self-ordered pointing task and the tower of London test in man [5,6]. Performance of all these tasks is impaired when the prefrontal cortex is damaged. Our hypothesis is that the prefrontal cortex is also 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 [1]. Unit recordings in this area during performance of the task could give access to the neural correlates of spatial reasoning.

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