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Ranking of memories and behavioral strategies in the radial maze

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Abstract. New features of actual choice behavior and effortful information processing in rats were demonstrated in an eight-arm radial maze through modifications of a matching-to-sample task. Two attempts were allowed for a squad of hooded Sprague-Dawley rats (*n*=7) for finding a reward in a testing phase of the task. The results showed flexibility and sooner learning to matching rule on the second testing attempt that was only later followed by an improvement of choice accuracy on the first attempt. "Hidden learning" on the second attempt could reflect memories and behavioral strategy, which were present, but not expressed on the first choice. The hypothesis was advanced that learning expressed on the second attempt reflects encoding of a matching rule, whereas improvement on the first choice reflects changes in the rank of acquired memories and behavioral strategy. A second experiment on the same squad of rats tested the ability of trained animals to rank already acquired memories. Following the introduction of the second sample to the study phase of the task, the rats learned to prefer to match the first sample in the testing phase, rearranging ranks of stored memories under the internal control of win–stay strategy. Alternative explanations of interference, trace decay and ranking were compared in order to account for the present results.

Key words: actual choice, ranking of memories, radial maze, working memory, matching-to-sample

INTRODUCTION

Although major progress had been made in discovering the features and neurobiology of spatial working memory, the mechanisms of memory-dependent actual choice behavior and effortful information processing are still largely unknown (Bouton 2002, Dallal and Meck 1990, Granon et al.1994, Grigorian and Stolberg 1992, Hudon et al. 2002). More refined investigation of these mechanisms is the key to understanding the effects of stress on memory-dependent choice, normal and pathological functioning of the brain, which underlie complex forms of behavior (Bouton 2002, De Rosa et al. 2004, Hammar 2003, Luine 2002, Payne et al. 2002, Thinus-Blanc et al. 1998). One of the most promising tools for analysis decision-making and effortful information processing in animals is undoubtedly the radial maze (Brown 1992, DiMattia and Kesner 1984, Hunt et al. 1994, Jakubowska-Dogru et al. 2003, Olton 1979, Olton and Samuelson 1976, Olton et al.1992, Stolberg and Roberts 1995).

From the very beginning, experiments on the radial maze have shown that exclusive spatial memory in rats could be assessed only with win–shift tasks (Gaffan and Davies 1981, Haig et al. 1983, Olton and Schlosberg 1978). Early attempts to train rats to solve win–stay tasks on the radial maze failed (Gaffan and Davies 1981, Olton and Schlosberg 1978). To account for the data that seemingly contradicted the associative learning paradigm, Olton assimilated an ecological model of optimal foraging in natural habitats (Olton and Schlosberg 1978, Olton et al.1992). This model was based on field data, according to which predators follow one of two main strategies after finding food: returning to the initially visited site (win–stay) or going to the new location (win–shift). Olton and Schlosberg (1978) suggested that rats are genetically predisposed to use win–shift foraging strategy, and since the requirements of the win–stay task counter to natural tendency, rats learn these tasks poorly.

As a result, for a long time, the radial maze was not considered suitable for matching-to-sample studies and the main body of developmental, neurophysiological and behavioral experiments on memory in rats was performed using win–shift tasks (Brown 1992, Granon et al. 1994, Mair et al. 2003, McDonald and White 1993, Olton et al. 1992, Wan et al. 1994).

Yet, in some experimental conditions, win–stay learning of rats on the radial maze had been demonstrated. It was shown that when all of the alternatives are familiar or when the food remains non-depleted after each arm visit, rats do learn win–stay tasks (Gaffan and Davies 1981, Gaffan et al. 1983). Roberts and Dale (1981) showed that when rats were exposed to massed training on a win–shift task, the memory of arm visits from previous trials caused a proactive inhibition effect. Olton himself found that rats are able to develop a win–stay learning set (Zeldin and Olton 1986).

In addition, it was found that win–stay trained rats differ from the win–shift trained ones in their patterns of both choice and memory properties (DiMattia and Kesner 1984, Kesner et al. 1988). In a task, involving memory for a serial list of arms entered, win–stay trained rats showed a serial position curve, containing both primacy and recency effects, whereas win–shift trained subjects, demonstrated only recency, but no primacy effect (DiMattia and Kesner 1984). Authors ascribed generation of primacy effects to more extensive and prolonged activation of memory traces in rats, trained to win–stay. They suggested that these findings could be explained by the theory of automatic *versus* effortful information processing (Hasher and Zacks 1979). They argued that learning to match or win–stay, involved effortful processing, while win–shift was an innate behavioral predisposition and involved automatic processing. Therefore, in order to learn the matching rule, which places a considerable load on memory and requires elaborative response selection, effortful information processing should predominate over inborn and automatic strategies.

A further contribution to an understanding of effortful information processing was made in experiments, combining special modification of matching-to-sample task with the advantages of multi-arm mazes (Roitblat and Harley 1988). A typically matching-to-sample task implies exposure of the subject to a sample stimulus in the study phase and a single attempt to match the sample among alternatives in a testing phase. An essential feature of the modification was that in a testing phase of the task, rats were given an additional second choice after a first-choice error. According to this procedure, rats were forced to enter one arm as a sample in a study phase and then were required to choose among all three arms with a choice of only the sample arm rewarded. If an error was made, the rat was given a second choice between the two remaining arms.

It was found that after an error, rats chose the sample arm on the second choices far above a chance level of

50%. Correct second choices after incorrect first choices, discredit the all-or-none theory of encoding and suggests that memory of the sample exists and persists, even though an incorrect initial choice was made. Surprisingly, however, when rats were given a second choice with all three arms available, they tended to repeat their initial erroneous response. Only when they were given a choice between the remaining two arms, did they reveal behavior optimization, and choose the sample above chance accuracy, following first choice error (Adams-Pepper et al. 1992). It was concluded that rats tended to persevere and showed the lack of flexibility on the second choice, because of their failure properly to encode the location of the sample. These experiments introduced a second choice in a testing phase of the matching task as a very useful analytic tool, but they did not use this tool fully for the study mechanisms of actual choice.

It could be suggested that single choice reaction on the second attempt (Adams-Pepper et al. 1992, Roitblat and Harley 1988) might not be a sufficiently sensitive procedure for discovering behaviors, which were not expressed during the first choice. The limitations are imposed by limited feedback on outcomes: the rats could not correct their errors during the second attempt and not every trial ended in a reward. It is possible that retrieval failure and not encoding caused perseverance and lack of flexibility in the second choice (Adams-Pepper et al. 1992). One of the questions, which the present study came to address, is whether the limitations for expression of sample memory on the second attempt could be overcome, despite the multiple alternatives on the radial maze. For this purpose, the flexibility of behavior on the second attempt and the hypothesis of retrieval failure were tested by providing rats with more feedback, giving them an opportunity to correct errors and find a reward on each trial. A comparison of the patterns of errors on the first and second testing attempts over acquisition trials was made to reveal the succession of decision processes throughout the stages of learning.

As the natural foraging tendency of rats is to shift after finding reward, matching-to-sample task, requiring effortful information processing, was chosen to test the correlation between win–shift and win–stay strategies during acquisition of the skill. The aim of the study was to make visible the sequence of changes in decision-making, using two testing attempts and stage analysis of the learning curve as analytic tools.

METHODS

Animals

The subjects were seven experimentally naive hooded male Sprague-Dawley rats.

On arriving in the laboratory, rats were approximately 100 days of age and weighed about 300 g. They were housed in individual cages under a 14/10 light/dark regimen with free access to water. Throughout training, the rats were maintained on 24-hour food deprivation cycle with regularly scheduled post training feedings with Purina Rat Chow to maintain them on approximately 85% of their free feeding weights.

For the second experiment the squad of the same seven rats, trained to matching-to-sample task was used.

Apparatus

Rats were tested on the elevated eight-arm radial maze. The maze was constructed of plywood and painted with black paint. It was raised 91.5 cm off the floor and had an octagonal center compartment 47 cm across. Eight arms radiated from the central compartment at 45 degrees from each other. Each arm was uncovered, 80 cm long and 10 cm wide. The entrance segments of the arms were bordered with 15 cm long and 10 cm high walls to prevent climbing between the arms. One out of the eight arms served permanently as a starting compartment, whereas the other seven served as goal arms. The starting compartment and each goal arm were separated from the rest of apparatus by guillotine doors. The experimenter sat near the arm, which served as the starting compartment and operated the guillotine doors by means of a cord.

In the experiments carried out, conditions were created, facilitating win–stay learning.

It had already been demonstrated that when rats do not deplete source of the food, they return to it more easily than when the food is completely depleted (Gaffan et al. 1983, Haig et al. 1983). In the present study, non-depletion was used in all experiments as a condition to promote win–stay learning.

A food cup 3.5 cm in diameter and 3.25 cm deep was located 3.5 cm at the end of each goal arm, approximately equidistant from each side. The food cup contained false and true bottoms, baited with a piece of cheese before the trial. In the study phase, rats picked up two Noyes pellets and smelled the cheese through the hole in the false bottom. On the test phase, free access to the true bottom was allowed. The maze was kept dry throughout and was cleaned during and after testing each animal.

Learning sessions were conducted in a well-lit room, containing a window and door on the opposite sides of the room, TV and video player and other odds-and-ends typically found in animal laboratories. The free behavior of the rats in each trial was videotaped by an overhead camera mounted on the ceiling directly above the center of the maze.

Behavioral procedure

Pretraining was held on an elevated runway, which consisted of a starting compartment, a middle area and a goal arm with a food cup in the end. The middle area was separated from the starting compartment and the goal arm by the guillotine doors, which were manually operated by the experimenter. The door to the goal arm was open from the very beginning of the trial and was closed when the animal grasped its reward.

Each trial consisted of two runs: the reward for the first run was two Noyes pellets and the second run was rewarded by cheese. Pretraining was finished when each rat had made 10 successful trials.

Sessions of training were held on an eight-arm starburst radial maze once every 48 hours and each session contained seven trials. One arm of the maze was designated as the starting arm. The experiment combined use of the eight-arm maze with the second-choice procedure, invented in Roitblat's laboratory (Adams-Pepper et al. 1992, Roitblat and Harley 1988). Each trial consisted of two phases (Fig. 1). In the study phase, the animal visited a randomly chosen sample arm in a forced-choice run, while the doors on the remaining six arms were closed. In the testing phase, the rat had to match the sample in one or two free-choice attempts (all the arms were opened).

During the study phase, at the end of sample arm, there was a food cup baited with two Noyes pellets and cheese under the false bottom. The rat was allowed to eat two 45-mg Noyes pellets on the false bottom and to smell a piece of cheese placed below it through a hole in the false bottom. Thus, the food available in the target arm was not depleted in the study phase.

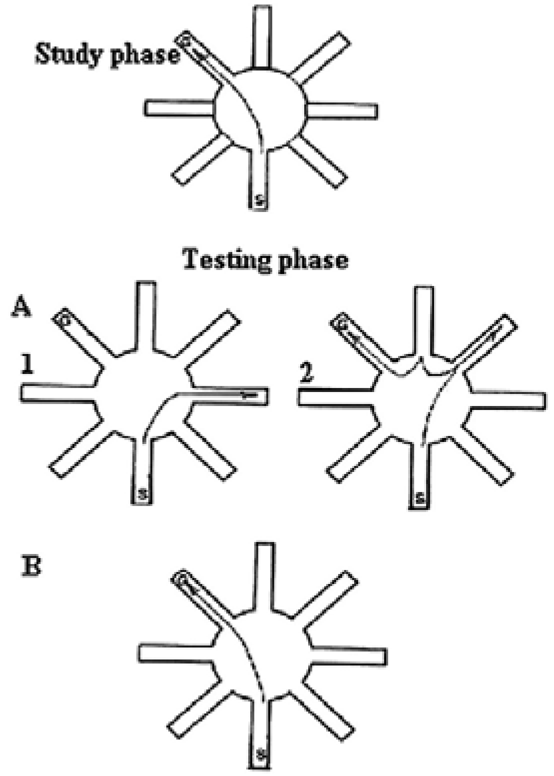

Fig. 1. Scheme of the apparatus and the behavioral procedure in a matching-to-sample task. Each trial consisted of two phases. In the study phase, only one randomly chosen sample arm was opened. An animal visited it from the starting compartment (S). The reward for this run was two Noyes pellets, combined with smelling the cheese under the false bottom (G). In the testing phase, all of the arms were opened. Only one target arm was rewarded by cheese (G). The figure illustrates two different experimental situations (A and B), which depend on the choice accuracy in the first testing run. If the rat entered the non-target arm (A1) in a first testing choice, the experimenter returned it to the starting compartment (S) and allowed unlimited free search in a second attempt (A2). If the rat chose correctly (B), it consumed the cheese and the trial was ended.

After the forced-choice run, the rat was gently returned by the experimenter to the starting arm for testing and was allowed a free choice among all of the seven open arms. If the rat chose correctly (i.e., returned to the target arm), it consumed the cheese and the trial was ended. If it entered a non-target arm, the experimenter returned the rat to the starting arm and allowed unlimited free choice in a second attempt. The mean number of arms visited at the second attempt was counted using the following scheme. If the rat entered the sample arm on the first choice, the trial was ended and the score for the second attempt was zero (Fig. 1, case B). If the sample arm was not chosen first, the score for that trial was the total number of arm entries in the second attempt (Fig. 1, case A, score = 2).

The VCR continuously monitored the animals' behavior and, after the experiments, the data were analyzed using videotaped records. Episodes of approach and visual orientation toward the arms without visiting them were classified as microchoices (Brown 1992). Visiting the arm was considered a choice.

The trained rats were tested in experiment on memory retention with delay. After a sample run, the experimenter took the rat from the maze to a special cage for 60 seconds delay and then returned it to the maze for the testing run. The rats were tested once every two days with seven trials in a daily session. Each arm was rewarded once and in random order.

As the training-to-matching task was completed, the experiment was designed to test the ability of the rats to build hierarchies of stored memories and rearrange them.

In the study phase of the task, the second sample was introduced. This sample was false and it was not rewarded by cheese in the testing phase. Each rat was forced to visit two different sample arms in two consecutive runs from the starting arm in the study phase of each trial. At the end of each sample arm, an animal was rewarded with two Noyes pellets, but it could only smell the cheese under the false bottom in the first sample arm. In the testing phase, each rat was allowed free choice among all of the seven arms. Only a return to the first of the two sample arms yielded a cheese reward (Fig. 4). As in previous experiment, the rats received two testing attempts to find the reward. The most recently visited sample had become the source of interference and animals had to learn to ignore it and prefer the first sample, next to the most recently visited one. Rats were tested with seven trials in daily sessions every two days and each arm was rewarded equally and in random order. Adjacent arms were never baited as sample arms (Fig. 4).

Statistics

ANOVA with repeated measures and two within-subject factors (correct choices in first attempt × number of visits in second attempt) was used to compare performance at the first and second attempts in the early stage of learning. The subsequent acquisition of matching rule at the first attempt and the dynamics of changes in number of microchoices were assessed by one-way ANOVA with repeated measures.

In the second experiment, the interaction in matching to first and second samples over the learning span was measured by ANOVA with repeated measures and two within-subject factors (first sample choices × second sample choices). Acquisition of the skill to match the next-to-most recently visited arm was computed with one-way ANOVA. *Post hoc* Bonferroni comparisons were applied in the second experiment. All of the statistics were compiled, using the SPSS statistical package from Tel Aviv University.

RESULTS

Acquisition of matching-to-sample

The acquisition data were plotted across daily blocks of seven trials for two measures of performance (Fig. 2). ANOVA with repeated measures and two within-subject factors showed significant interaction between learning on the first and second attempts during the first seven blocks ($F_{6,36}$=2.66, P<0.05). A drop in the number of arm entries during the second attempt occurs before any significant increase in accuracy on the first choice. The main effect of repeated measures at Block 7 was found to be significant and showed learning on the second attempt ($F_{6,36}$=2.78, P<0.05). A significant rise in choice accuracy on the first attempt appeared later.

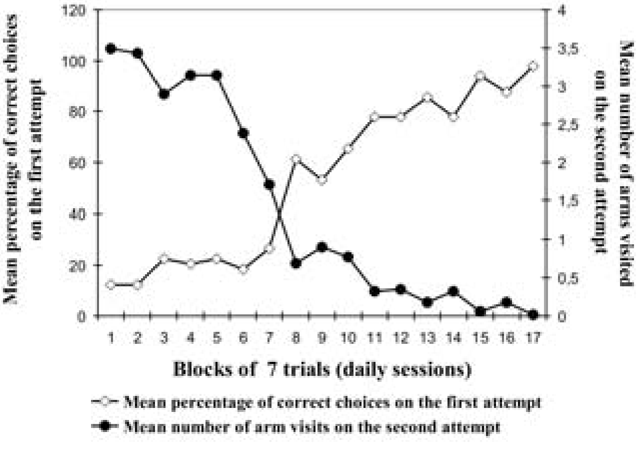

Fig. 2. Acquisition of matching-to-sample in the radial maze. The descending curve refers to the right ordinate and plots the number of arms visited before entering the sample arm. The curve shows that the number of arm entries started to drop at Blocks 6–7 and remained at a low level throughout the remaining blocks. The ascending curve plots the variable shown on the left ordinate, the percentage of the correct sample arm entries made on the first choice. This curve stays at a near chance level over Blocks 1–7, but rises to 60% accuracy on Block 8. It then rises consistently and achieves an almost perfect matching score in the final block of trials (Blocks 8–17).

One-way ANOVA with repeated measures for Blocks 8–17 showed significant effect of blocks to choice accuracy at the first attempt ($F_{11,66}$=4.36, P<0.001).

The fact that the curve for the number of arms visited drops significantly before the increase in accuracy of the first choice is an important aspect of these data. Only after a significant reduction of the search of the sample arm on the second attempt do rats adopt the matching rule that specifies a return to the most recently visited arm on the first choice. At this stage, win–stay behavior prevails over win–shift and changes its rank in the hierarchy of behavioral strategies (Fig. 2).

The next graph (Fig. 3) compares the acquisition of a matching skill at the first testing attempt with another measure of performance – microchoices. Microchoices involve a clear approach and orientation toward an arm that may not then be followed by an arm entry (Brown 1992). One-way ANOVA with repeated measures over the whole span of learning on the first choice revealed a significant increase in the mean number of microchoices as training progressed ($F_{16,96}$=8.36, P<0.001).

Matching skill was found to be resistant to a 60 seconds delay between the study and test phase of the matching task. One-way ANOVA with repeated measures showed no significant effect of the delay on sample memory retention and performance in the testing phase ($F_{3,18}$=1.0, P>0.4)

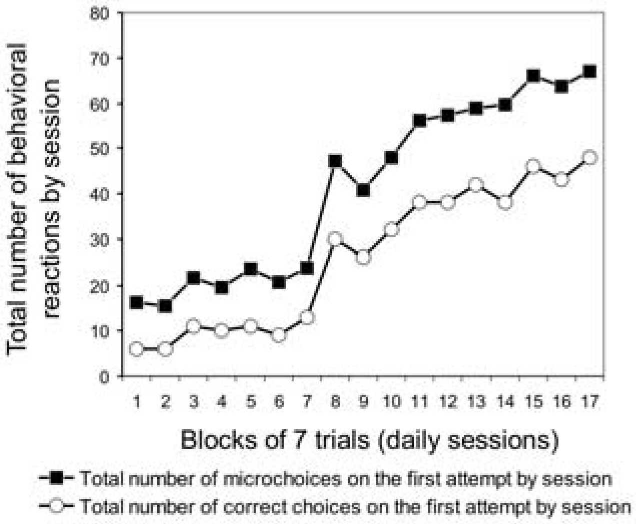

Fig. 3. Parallel rise in the mean number of the microchoices and the correct choices on the first attempt. Rats adopt stricter criteria for entering arms as they learn the matching rule. Notice that the overall number of the microchoices, shown on the left ordinate, begins to rise on Block 8, the same block on which first-choice accuracy starts to improve. The learning of the task does not influence the direction of the microchoices.

Retroactive interference and test for ranking

In order to test the ability of animals to use and rank already acquired memories a second experiment was designed. A second sample was introduced in the study phase of each trial. The rats visited two different sample arms in two separate forced-choice runs of the same trial. In the testing phase, the most recently visited sample became a non-target arm. Thus, conditions of retroactive interference were created and animals had to learn to overcome it and to prefer the first sample to the second (Fig. 4).

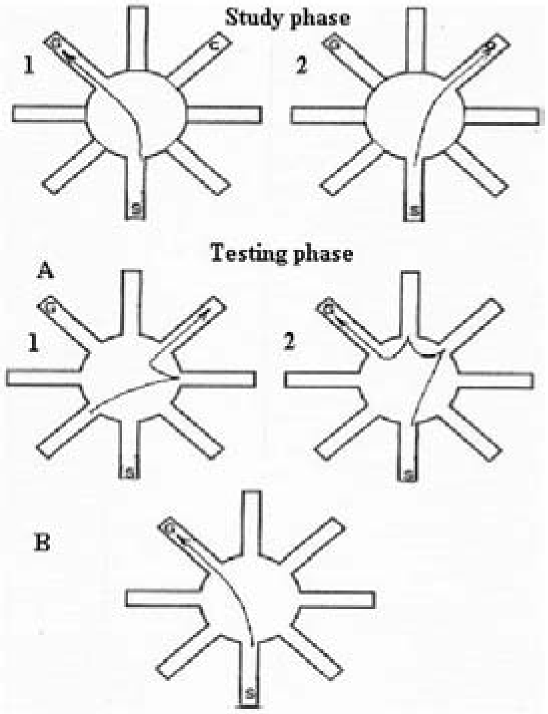

Fig. 4. Scheme of the behavioral procedure in the test on overcoming retroactive interference. The study phase consisted of two separate forced-choice runs to the sample arm (1) and to the second false sample arm (2). The reward for the first run (1) was two Noyes pellets combined with smelling cheese under the false bottom (G). The reward for the second forced-choice run (2) was two Noyes pellets without smelling cheese (G). In the testing phase, all of the arms were opened. Only one target arm was rewarded by cheese (G). The figure illustrates two different experimental situations (A and B), depending on the accuracy of the first testing choice. If the rat entered the non-target arm (A1), it was returned to the starting compartment (S) and given a second testing attempt (A2). If the rat chose correctly (B), it consumed the cheese and the trial was ended.

Performance data are plotted on Fig. 5. The choice of the first sample arm (the next to last sample visited) rose progressively after Block 5 to about 65–70%. ANOVA with repeated measures and two within-subject factors for the Blocks 5–10 showed significant interaction between the choice of first and second sample arms in the testing phase ($F_{5,30}$=4.85, P<0.01).

One-way ANOVA with repeated measures for the whole span of learning (Blocks 3–10) showed that the increase in choice accuracy was highly significant ($F_{7,42}$=5.36, P<0.001). *Post hoc* Bonferroni comparisons showed significance in both effects.

Restoration of dominant rank for the memory of most recently visited entry is plotted in Fig. 6. One-way ANOVA with repeated measures showed the significant effect of repeated measures for Blocks 1–6 ($F_{5,30}$=3.76, P<0.01).

DISCUSSION

Matching-to-sample on a radial maze is an appropriate task for investigation of the mechanisms of memory-dependent actual choice and effortful information processing in rats (Adams-Pepper et al. 1992, DiMattia and Kesner 1984, Hunt et al. 1994, Kesner et al. 1988, Roitblat and Harley 1988, Stolberg and Roberts 1995). The findings of this experiment led to the proposal of a model of matching-to-sample acquisition, with three stages:

1. Rats initially have a strong win-shift bias, which is opposed weakly by a tendency to return to the non-depleted sample arm.
2. As training proceeds, the win-stay tendency gradually appears on the second attempt. It suggests that the rats' tendency to avoid recently entered arms weakened as the trials continued, leading to sample arms having higher rank in the hierarchy of arm preferences.
3. Adoption of matching behavior, based on the most recent arm entrance in the first choice appears after a significant reduction of visits to non-target arms on the second attempt and improves consistently to an almost perfect matching score (Fig. 2).

Data show that the associative mechanism does not contradict optimal foraging model much, presenting the best explanation for current results. In present experiments, win-shift behavior as inborn foraging strategy in rats appears first in the course of learning, while win–stay foraging behavior appears later and should be viewed as totally learned. Thus, associative memory operates in a classical way, in that rats prefer places associated with food, to those associated with no food. On the other hand, working memory operates on a certain genetic background, which is the inborn bias to a shift during foraging in a multi-alternative environment.

New features of early learning and effortful information processing in rats were found in this experiment. Thus, early stage of training represents phenomenon of "hidden" learning, concealed in the depth of memory, which, at the second attempt, permits visualization. It appears that a significant drop in number of visits to non-target arms on the second attempt reflects the encoding of the matching rule. Subsequent expression and transfer of win–stay behavior to the first choice reflects not only an increase in its relative strength, but also a parallel change in the rank of acquired strategy.

Current findings may best be explained by a model that suggests that animals make decisions about arm entries based on the ranking of arm memories.

The model holds that arm memories are ranked for entrance based upon the recency of arm entrance. During the early stages of learning, a recently entered arm is placed late in the ranking, whereas arms not entered recently are placed early in the ranking (win–shift tendency). As training proceeds, the rank of recently entered arms gradually moves from later to earlier ranks, until it finally occupies the first rank (win–stay tendency). This model explains why the number of arms entered at the second attempt dropped before the accuracy of first choices improved. As the rank of the sample arm entered moved to earlier ranks, the number of arms entered before entering sample arm should decline. However, a decline in first choice errors would not appear until the memory of the sample arm begins regularly to occupy the earliest rank. Finally, as the win–stay strategy yielded earlier rewards, it eventually changes its rank and dominates performance on first choices, leading to near-perfect accuracy on the first choice in late phase of learning.

The ability of rats simultaneously to retain several working memories and to rebuild ranks of stored memories was tested under conditions of retroactive interference.

A second sample was introduced to trained rats in the study phase of the task. Because this sample was not reinforced in the testing phase by cheese, it was a false sample. Rats had to learn to ignore this and to prefer the first sample, which was the next-to-most recently visited arm.

It is well known that the acquisition of new learning is frequently challenged by interference, which occurs when previous learning disrupts later learning or later information interferes with earlier learning. The concept of interference implies that following the introduction of a false second sample, the latter will interfere with performance and no new learning will occur. Can rats overcome interference? If the answer is yes, what concept can better predict performance of rats during relearning?

According to another concept – trace decay, the second false sample should permanently decrease choice accuracy on the first testing attempt, leading to forgetting the location of previous sample arms, memories of which should not influence behavior.

In contrast to concepts of trace decay and retroactive interference, which predict a permanent decrease in choice accuracy without relearning, advanced here is a model of ranking that predicts that rats should be able to relearn, due to the rearrangement of hierarchies of acquired memories. Their performance should not become random, but working memories and the matching rule should control it. The experiment served as a direct test to all three concepts.

Results show that rats are able to solve this task and their behavior is controlled by several working memories (Fig. 5). Rats can be trained to match a next-to-recent arm entry and not just the most recently visited arm entry. They are able simultaneously to retain several working memories and solve the task, rearranging preferences of matching between two sample arms as the learning proceeds. Although a second false sample effectively caused interference, the effect was proved to be a temporary (Fig. 5). Hence, the interference effect could be viewed, as the initiation of change in the hierarchy of memories and the mechanism of overcoming interference is a rearrangement of ranks of stored memories.

Results suggest also that concept of the decay of memory trace, which predicts forgetting as a result of exposure to conditions of interference, is not always appropriate to explain decision-making in a multiple-choice situation. In fact, it seems to be inadequate to account for effortful decision-making in stress free situations.

Data show that three recent memories controlled the choice effectively on the basis of the matching rule and they determined most of the decision-making processes (Fig. 5).

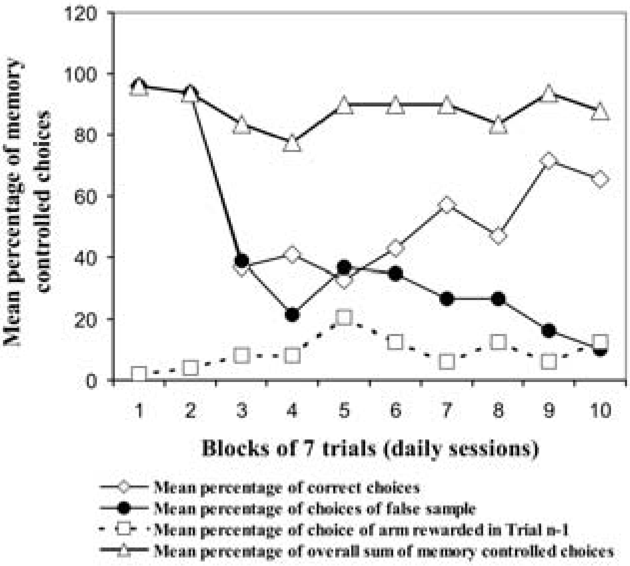

Fig. 5. Rats learn to ignore most recently visited arm, though they remember its location and their behavior is controlled by working memory and matching strategy. Four curves on the graph represent mean percentage choice of the first sample arm, second sample arm, the correct arm rewarded in Trial n-1 and total of these three memory controlled components. It can be seen that after introduction of second sample (Blocks 3–4), the sum of choices made by rats to this memory controlled three alternatives is not significantly different from the background performance (Blocks 1–2). Choice for the most recently visited sample arm dropped immediately after introduction of second false sample (Block 3). However, the mean percentage of choice for this arm until Block 5 was at the same level as choice of the target arm, which was rewarded by cheese (Blocks 3–5). After Block 5, matching to the target arm increased, while the choice of a non-target false sample decreased from about 35% to less than 10% (Blocks 5–10).

Acquired matching strategy is stable and resistant to changes in the reinforcement schedule. Canceling the second sample led to rapid restoration of the initial ranking. Rats returned to the strategy of matching the most recently visited arm, confirming existing evidence that extinction does not imply a destruction of the original learning. In contrast to the “unlearning” theory, current data support the approach presented by Bouton that extinction and retroactive interference involve new learning, which is stored together with the old (Bouton 2002).

The mechanism for restoring original learning can be explained by an adaptive flexibility of ranking processes, i.e., a capability to rebuild hierarchies of stored memories, according to a reinforcement schedule (Fig. 6).

When initial behavioral strategy is reinforced, then information processing is automatic and there is no need for effortful information processing. But when the ini-

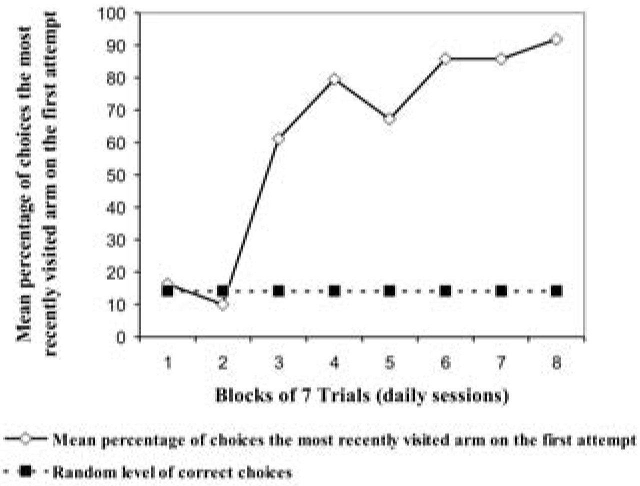

Fig. 6. Canceling the second sample leads to the rapid restoration of rank of memory for the most recently visited arm. Canceling the second false sample in the study phase of the task leads to immediate rise, but not full restoration of matching the most recently visited arm (Blocks 1–3). In the first daily sessions, rats chose the arm, rewarded in Trial n-1 at the level of about 30% (Blocks 3–5), though very rapidly the matching of the most recently visited arm prevailed completely (Blocks 6–8).

tial strategy is not reinforced, the effortful information processing is activated and it recruits the resources of memory, leading to a new examination of the contents of working memory, and allowing parallel processing of multiple memories and strategies. It appears that a change in rank is one of the distinctive features of effortful information processing, which is activated each time when initial strategy interferes with the reinforcement schedule.

An important question to be discussed here is whether performance in matching-to-sample is guided by list-like or map-like representations. Cognitive mapping implies the ability to extrapolate correct direction from the starting compartment. If cognitive maps guided performance, the number of microchoices should be significantly reduced with learning. However, the opposite is the case (Fig. 3). The direction of the microchoices becomes increasingly imprecise as rats master matching skill. At the same time, the correct rejection rate significantly increases during training. These results can be well accounted for by the approach developed by Brown on behavioral data with win–shift tasks (Brown 1992, Brown et al. 1993). According to this model, the choice process on a radial maze may be described as sequential and not simultaneous. Choice effectiveness depends on the nature of representations and the strictness of the choice criteria used by rats. Rats that have unrestricted access to visual stimuli use list-like and not map-like representations (Brown 1992, Brown et al. 1993). In current experiments, the higher the choice accuracy observed in the course of learning, the more imprecise microchoices became (Fig. 3). Rats did not acquire the ability to extrapolate the location of the sample from the starting arm and were guided by list-like representations and a sequential choice mechanism. They adopted more conservative, stricter criteria for arm entry, which led to a high rate of correct rejections and almost perfect matching score.

To sum up, the results demonstrated that ranking and rearrangement of ranks of stored memories and behavioral strategies is probably one of the important mechanisms for new learning and overcoming the effects of interference. They can become visible, when initial strategy is known and effortful information processing is required. The concept of ranking accounts for the data presented here better than do the models of trace decay and interference, which were traditionally used to explain memory-dependent choice behavior (Bouton 2002, Hudon et al. 2002). Both, the investigation of ranking, and the norm and pathology in the rearrangement of ranks, should be continued by computational, neurobiological and behavioral methods.

CONCLUSIONS

The acquisition of matching-to-sample on the radial maze has three stages.

Initially, rats have a strong win–shift bias, which is opposed weakly by returns to the non-depleted sample arm. As training proceeds, the win–stay tendency gradually prevails at the second attempt. Only after significant attenuation of the search for the sample arm on the second attempt, do rats adopt the matching rule that specifies that they return to the most recently visited arm on the first choice. At this stage, win–stay behavior prevails and changes its rank in the hierarchy of behavioral strategies.

Behavior at the second attempt of the matching task is flexible and shows learning of the matching skill sooner than first choice performance. The chance to correct errors at the second testing attempt activated effortful information processing and the ability to optimize behavior, despite the multiple alternatives. The perseverance effect at the second attempt was not observed.

Rats learn the matching rule, employing a sequential mechanism of choice and list-like representations. The learning of the task does not influence the direction of the microchoices. Ranking is reflected in a high rate of non-target arm rejections and stricter criteria for arm entry.

Rats that are trained to the matching rule can learn to overcome interference and match the first of two samples arms entered on the same trial. It can be suggested that the mechanism of this learning is the rearrangement of ranks of stored memories, based on stable and prevailing matching strategy. A task with two sample arms in the study phase for overcoming interference can be considered and further investigated as a specific ranking task.

Canceling the second sample in the study phase of the matching task leads to the rapid rearrangement and restoration of the dominant rank of memory for the most recently visited arm, under control of the win–stay strategy.

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