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D. S. Olton

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The temporal context of spatial memory

By D. S. Olton

Department of Psychology, The Johns Hopkins University, Baltimore, Maryland 21218, *U.S.A.*

Foraging strategies provide an effective and convenient means of investigating some characteristics of animal intelligence. The temporal and spatial distributions of food in the environment are not entirely random, and animals that use information about these patterns can gain an adaptive advantage over animals that do not. For some types of strategies to be effective, the animal must remember the temporal context of a visit to a spatial location and use this memory to make decisions about the current distribution of food in the environment. Experiments with different species (rat, Hawaiian honeycreeper, Marsh tit, Clark's nutcracker) have used variations of a delayed conditional discrimination to examine the cognitive processes influencing this type of memory. These include: primacy, recency, proactive interference, retroactive interference, decay, consolidation, and chunking. The results of these experiments provide information about the types of memory processes that animals use when searching for food, and illustrate the usefulness of combining psychological and ethological approaches when studying animal intelligence.

Every event that we wish to remember happens in a particular place at a particular time. For some types of decisions, all three of these components (the event, its spatial location, and its temporal context) must be associated together if their memory is to help the individual make the correct choice.

Animals are frequently confronted with these types of decisions in their natural environments (Krebs 1978). Resources are not distributed homogeneously. In any particular place, more resources are available at some times than at others. At any particular time, more resources are available in some places than at others. Furthermore, these temporal and spatial patterns are cyclical and predictable. Thus, a memory of the spatial and temporal context of previously experienced events can be useful in making decisions about the current distribution of resources.

Being in the right place at the right time confers an adaptive advantage. The animal increases the availability of resources, and decreases the cost of obtaining them. Thus, environmental pressures encourage the development of a memory system that can associate an event with its spatial and temporal context.

Environmental pressures favouring the development of an ability do not ensure that animals will indeed acquire this ability. The fossil record stands in mute but elegant testimony to the great probability of failure. However, empirical data demonstrate that many animals have developed this type of memory system. Convergent evolution in different species is strong evidence of a consistent environmental pressure, and this memory helps animals behave adaptively (that is, intelligently) in many different situations. My first example is from a laboratory discrimination task with the ubiquitous *Ratus norwegicus*. The subsequent examples are from naturalistic settings (real or simulated) with several other species. In all of these, the analysis involves answering the same three questions:

(i) is a memory of the temporal and spatial context of an event useful for accurate decisions about the current distribution of resources?

(ii) Do animals use this memory?

(iii) If animals do use this memory, what are the characteristics of it?

1. Radial arm maze

The test apparatus is a maze with arms radiating from a central platform. At the start of each trial, one pellet of food is placed at the distal end of each arm. Food is not replaced during a trial. Consequently, the optimal strategy for the rat is to visit each arm once and only once during a trial (Olton & Samuelson 1976).

A memory of the temporal context of a visit to each arm can help the rat to determine which arms currently have food. If an arm has not been visited during the current trial, that arm has food and the rat ought to go to the end of it. If an arm has been visited during the current trial, that arm no longer has food and the rat ought not to go to the end of it. Only by determining whether an arm has been visited during the *current* trial can a rat decide whether or not it has food. Visits to arms in previous trials must be distinguished from visits to arms in the current trial. A memory of the temporal context of each visit can help make this discrimination.

However, many relevant redundant strategies can be used to determine where food is located. These strategies use different discriminative stimuli and different types of memory. They are relevant because they can be used to choose correctly. They are redundant because with the usual test procedure the experimenter is unable to determine the extent to which each one actually directs choice behaviour. For example, intramaze stimuli from the food or from previous visits, and specific response patterns, can all lead to correct choices.

When relevant redundant strategies are available in a discrimination procedure, two steps can be taken to determine if an animal actually uses the particular strategy that the experiment wishes to study. First, the strategy of interest is made independent of all others. Second, only that strategy is made relevant. A comparison of choice accuracy in the modified task with that in the original task indicates the extent to which the animals can use only the single strategy to choose correctly.

Experiments with the radial arm maze were designed to force the rats to remember the temporal context of a visit to each food location and prevent them from using other strategies to determine where food was located. The rats still chose among the arms very accurately. Consequently, rats do use the memory of the temporal context of their visit to each spatial location to decide where food is located (Beatty & Shavalia 1980*a*; Maki *et al.* 1985; Olton *et al.* 1977; Olton & Samuelson 1976; Roberts 1979, 1981; Roberts & Dale 1981; Roberts & Smythe 1979; Walker & Olton 1979). Similar conclusions have been obtained from many other experiments with mazes (O'Keefe & Conway 1978; Olton 1979).

Identifying the characteristics of this memory requires close attention to experimental procedures and the logic of interpretation. Although the choices themselves can be observed and quantified without difficulty, using them to infer the characteristics of memory must proceed cautiously. For example, consider the problems that arise if response patterns are not eliminated. When leaving an arm and returning to the central platform, a rat usually turns in a particular direction (clockwise or counter-clockwise) and goes to an arm close to the one previously visited. Although these response patterns do not constitute a strategy that is required to choose correctly, they are still habits and bias choice behaviour (Olton *et al.* 1977; Roberts & Dale 1981). Inferences about memory are compromised because the experimenter cannot determine the extent to which any given visit is influenced by memory or by the variables controlling the response pattern. In short, the extent to which choice behaviour can be used to draw conclusions about memory is limited by the extent to which memory and only memory influences that choice behaviour.

Consequently, the following discussion of the characteristics of memory is based on only those experiments that used procedures designed to maximize the influence of memory on choice behaviour. In most cases, the relative salience of extramaze cues was enhanced by having an open maze in a well-lighted room with many distinctive extramaze stimuli. Sides were often placed along the edges of each arm to help the rat stay on the maze, but these were low enough to produce only a minimal impediment of the rat's ability to see the extramaze cues. In the best experiments, response patterns were prevented by a series of forced visits followed by a choice between two arms. For each forced visit, the rat was given access to only a single arm. Consequently, the experimenter, rather than the rat, chose which arms were to be visited and the order of those visits. After these visits, the rat was given access to two arms and allowed to choose between them. In other experiments, the rat was confined to the centre platform after each visit, or removed from the maze during the trial.

Primacy

Primacy is more accurate memory for items at the beginning of a list than for items in the middle of the list. With the usual win–shift response–reinforcement contingency described above, primacy did not occur. The probability of making an error (returning to an arm visited previously during a trial) was no less for the first arm visited that it was for arms visited in the middle of the trial (DiMattia & Kesner 1985; Kesner & Novak 1982; Olton & Samuelson 1976; Roberts & Smythe 1979). With a win–stay response–reinforcement contingency, however, primacy did occur; the probability of making an error to the first arm visited during a trial was less than that to arms that were visited in the middle of that trial (DiMattia & Kesner 1985).

Recency

Recency is more accurate memory for items at the end of a list than for items in the middle of the list. Recency did occur. The probability of making an error to an arm just recently visited was less than that for arms visited in the middle of a trial (DiMattia & Kesner 1985; Kesner & Novak 1982; Olton & Samuelson 1976; Roberts & Smythe 1979).

Proactive interference

Proactive interference is the deleterious effect of previously learned information on the ability to remember currently learned information. Proactive interference occurred within a trial on the same maze, between completed trials on the same maze, and between uncompleted trials on different mazes when all testing was completed in a relatively short period of time (less than 15 min). The probability of making an error increased as the number of arms visited before the one in question increased. The magnitude of the effect was small (if present) after a few visits. It was positively accelerated so that the magnitude of the effect was substantial after many visits (Roberts 1981; Roberts & Dale 1981). Interference was not produced by stimuli unrelated to those around the maze (Maki *et al.* 1979).

Retroactive interference

Retroactive interference is the deleterious effect of currently learned information on the memory of previously learned information. Retroactive interference occurred within a trial on the same maze, and between uncompleted trials on different mazes. The probability of making an error increased as the number of visits following the initial visit to an arm increased. The magnitude of the effect was minimal (if present) after a few visits and was positively accelerated (Beatty & Shavalia 1980*b*; Maki *et al.* 1979; Roberts 1981). Interference was not produced by stimuli unrelated to those around the maze (Maki *et al.* 1979).

Decay

Decay is the progressive deterioration of the memory with the increasing passage of time following the event to be remembered. Decay can never be completely isolated from interference due to events because events always occur as time passes. In these experiments, however, each rat was placed in a holding cage for the delay interval. Thus, the intervening events were minimized and were not visits to arms on mazes as in the previously described studies examining interference. Decay occurred. The probability of making an error increased as the time from the initial visit to that arm increased. This effect was minimal (if present) with delays of up to several hours and was positively accelerated (Beatty & Shavalia 1980*a*, *b*; Gaffan & Davies 1981; Knowlton *et al.* 1985; Roberts 1981; Roberts & Dale 1981; Roberts & Smythe 1979).

Consolidation

Consolidation is the decreased susceptibility of memory to disruption as the length of time following the information to be remembered increases. Consolidation did not occur within 8 h. The probability of making an error was just as great when 8 h intervened between the initial visit to an arm and the disruptive event (electroconvulsive shock or intrahippocampal stimulation that produced seizures) as when only a few seconds intervened (Knowlton *et al.* 1985; Shavalia *et al.* 1981).

'Chunking'

'Chunking' is the organization of information to be remembered so that it can be remembered more efficiently. A retrospective memory of the arms that have been chosen may be used at the beginning of a trial, while a prospective memory of the arms that are to be chosen may be used at the end of a trial. This shift from a retrospective memory to a prospective memory can reduce the number of visits that have to be remembered at any one time (although it adds the additional requirement of determining which type of memory is currently being used) (Cook *et al.* 1985). Organization of visits on the basis of the spatial location of the arms did not occur (Olton & Samuelson 1976).

2. NATURALISTIC SETTINGS

In each of the following examples, an animal was tested with commonly consumed food in either the natural habitat or a simulation of it. The discrimination problem facing the animal was one in which the memory of the temporal context of a visit to a spatial location could help determine the current location of food. The animals did use this type of memory to help decide which location should be visited: cues from the food itself or response patterns were not necessary for accurate choices. The controls to emphasize the use of memory and describe its characteristics were not as stringent as in the experiments with rats, and only some of the characteristics of the memory used by these animals have been identified.

Loxops virens

The Hawaiian honeycreeper, *Loxops virens*, obtains nectar from flowers of the Mamane tree, *Sophora chrysophylla*. During each visit to a flower, the bird removes all the nectar. The flower takes several hours to replace this nectar. During this time, the optimal strategy for the bird is to avoid just previously visited flowers and search elsewhere. Although the accuracy of choice behaviour of the birds varied from day to day, the probability of returning to a previously visited cluster of flowers was slightly less than that expected by chance. Substantial forgetting took place for visits to flowers several hours after the visit occurred. The variables responsible for this forgetting were not identified (Kamil 1978).

Parus palustris

Marsh tits, *Parus palustris*, store seeds in scattered locations and retrieve them many hours later. (This type of hoarding should minimize the probability of other birds stealing the seeds). After the birds have stored the seeds, the optimal strategy is to go to each location containing a seed once and only once, obtaining the seed from it on the first visit. A naturalistic environment was created in an aviary. Twelve small 'trees' were made from the limbs of real trees. Holes were drilled into the limbs. A piece of black cloth was stapled above each hole and could be lowered to cover the hole preventing the bird from seeing if a seed was located in the hole (Shettleworth & Krebs 1982).

At the beginning of each trial, a container of seeds was placed in the aviary. For the *hoarding* phase of the trial, the bird was released into the aviary and permitted to store these seeds. The bird was then removed from the aviary. For the *recovery* phase of each trial, the container of seeds was removed and the bird was allowed to search for seeds in the holes in the trees.

The choice accuracy of the birds during the recovery phase was very high, and remained significantly above chance even after 30 seeds had been obtained. This accuracy did not result from fixed search paths or discriminative stimuli from the food itself. The probability of a correct choice descreased as the number of choices during the recovery phase increased; because the interval between the hoarding phase and the recovery phase was long (several hours) compared with the interval for the storage of all the seeds in the hoarding phase (about 10 min), interference was more likely than decay.

Nucifraga columbiana

Clark's nutcrackers, *Nucifraga columbiana*, store many thousands of seeds from pine cones during the short time that these are available and then retrieve them during the subsequent year. After the hoarding of the seeds is completed, the optimal strategy for the nutcrackers is to visit each location of hoarded seeds, obtain the seeds there, and then not return. Observations of the birds in the natural environments suggest that they are very accurate in the choices of places to go to recover seeds (see review in Kamil & Balda 1985).

The aviary had a floor with 180 holes in it. In each hole was a cup full of sand. A wooden plug could be placed over the cup to prevent the bird from getting access to the cup. Rocks and boards were distributed around the floor to provide stimuli distinguishing the spatial locations of the different cups. In each of three *caching* sessions, a container of seeds was placed in the aviary and 18 of the holes were open. The bird was allowed to store seeds in only these sites. During the subsequent *recovery* session, the container was removed, all holes were opened, and the bird was allowed to choose among them (Kamil & Balda 1985).

The probability of going to a hole in which seeds had been placed remained above the levels expected by chance throughout the recovery session, but decreased more rapidly as the number of holes visited increased. Because the interval between the last caching session and the recovery session (ten days) was only slightly longer than the interval between the first and the last caching session (four days), this pattern may have been due to either interference or decay. When the birds made an error, they had a high probability of going to a hole adjacent to one in which seeds were stored.

3. Discussion

Animals do remember the temporal context of a visit to a spatial location and use this information to make decisions about the current distribution of resources in their environment. For rats solving a discrimination task in the laboratory, the parameters influencing the accuracy of this memory are essentially the same as those influencing human memory. For other animals in naturalistic settings, fewer parameters have been examined, but these also affect memory in the same way as they do in people.

These similarities suggest that analogous memory systems are present in all of these species. If such is the case, differences in the ability to remember information must result from quantitative variations in the shapes of the functions relating the parameters to memory rather than from qualitative differences in the types of parameters that influence memory.

These experiments indicate the advantage of combining two different perspectives: that commonly taken by psychologists when investigating memory in laboratory discrimination tasks, and that taken by ethologists when investigating optimal foraging in naturalistic settings. The psychological perspective provides information about the characteristics of memory and the types of experimental designs that can be used to investigate it. The ethological perspective provides information about the types of problems that animals face in their natural habitats and the ways in which memory can help solve them.

Historically, laboratory procedures have had more controlled experimental designs than those in naturalistic studies and these designs have permitted more definite conclusions about the variables that influence behaviour. However, laboratory experiments have often ignored the extent to which the task is meaningful to the animal being tested. Ultimately, every comparative study must justify its choice of task, and the major step in assessing the validity of any task is a comparison of its demands with those experienced by the animal in its natural habitat. Consequently, the most productive experiments are likely to be those that incorporate the advantages of experimental control into naturalistic settings. Some characteristics of the experiments reviewed in the last part of this chapter represent an excellent first step in this direction.

However, many questions remain to be answered. The representation of both the temporal (Church 1984; Gibbon *et al.* 1984) and the spatial codes (O'Keefe & Nadel 1978) remains to be identified, along with the ways in which these are associated together. A comparative study that goes beyond the experimental parameters influencing choice accuracy is necessary to determine the cognitive processes supporting this memory. Although the basic neuronal elements in the brains of birds and mammals are the same, their organization into ganglia and nuclei is very different. The question is whether the memory processes described for each of these species arise from the common neuronal elements or the different neuronal organizations. If the former, the psychological as well as the neurological mechanism involved in memory may be homologous, sharing the same origin. If the latter, both mechanisms are analogous, achieving the same goal through different means.

Finally, the spatial distribution of many resources other than food change with predictable temporal patterns, and those patterns can be much more complex than ones described here. Although relatively complicated schedules of reinforcement have been investigated in laboratory operant boxes, they have only begun to be studied in ethologically relevant settings. Thus, experiments need to address the broader issue of how animals allocate their time and energy among all the activities available to them. In this allocation, remembering the temporal context of a visit to a spatial location will help the animals choose intelligently among the various alternatives.

References

Beatty, W. W. & Shavalia, D. A. 1980*a* Spatial memory in rats: time course of working memory and effect of anesthetics. *Behav. neural Biol.* **28**, 454–462.

Beatty, W. W. & Shavalia, D. A. 1980*b* Rat spatial memory; resistance to retroactive interference at long retention intervals. *Anim. Learn. Behav.* **8**, 550–552.

Church, R. M. 1984 Properties of the internal clock. *Ann. N.Y. Acad. Sci.* **423**, 566–582.

Cook, R. G., Brown, M. F. & Riley, D. A. 1985 A flexible memory processing by rats: use of prospective and retrospective information in the radial maze. (Submitted).

DiMattia, B. V. & Kesner, R. P. 1985 Serial position curves in rats: Automatic vs. controlled information processing. (Submitted.)

Gaffan, E. A. & Davies, J. 1981 The role of exploration in win-shift and win-stay performance on a radial maze. *Learn. Motiv.* **12**, 282–299.

Gibbon, J., Church, R. M. & Meck, W. H. 1984 Scalar timing in memory. *Ann. N.Y. Acad. Sci.* **423**, 52–77.

Kamil, A. C. 1978 Systematic foraging by a nectar-feeding birds, the amakihi (*Loxops virens*). *J. comp. Physiol. Psych.* **92**, 388–396.

Kamil, A. C. & Balda, R. C. 1984 Cache recovery and spatial memory in Clark's nutcrackers (*Nucifraga columbiana*). *J. exp. Psychol.: Anim. Behav. Process.* (Submitted.)

Kesner, R. P. & Novak, J. M. 1982 Serial position curve in rats: Role of the dorsal hippocampus. *Science, Wash.* **218**, 173–174.

Knowlton, B., McGowan, M., Olton, D. S. & Gamzu, E. 1985 Hippocampal stimulation disrupts spatial working memory even after eight hours for consolidation. *Behav. neural Biol.* (Submitted.)

Krebs, J. R. 1978 Optimal foraging: Decision rules for predators. In *Behavioural ecology: An evolutionary approach* (ed. J. R. Krebs & N. B. Davies), pp. 23–63. Oxford: Blackwell Scientific Publications.

Maki, W. S., Beatty, W. W., Hoffman, N., Bierley, R. A. & Clouse, B. A. 1985 Evaluation of nonmemorial influences on rats' performance in the radial-arm maze with long retention intervals. *Behav. neural Biol.* (Submitted.)

Maki, W. S., Brokofsky, S. & Berg, B. 1979 Spatial memory in rats: Resistance to retroactive interference. *Anim. Learn. Behav.* **7**, 25–30.

O'Keefe, J. & Conway, D. H. 1978 Hippocampal place units in the freely moving rat: Why they fire where they fire. *Exp. Brain Res.* **31**, 573–590.

O'Keefe, J. & Nadel, L. 1978 *The hippocampus as a cognitive map*. Oxford: Oxford University Press.

Olton, D. S., Collison, C. & Werz, M. A. 1977 Spatial memory and radial arm maze performance of rats. *Learn. Motiv.* **8**, 289–314.

Olton, D. S. & Samuelson, R. J. 1976 Remembrance of places passed: Spatial memory in rats. *J. exp. Psychol.: Anim. Behav. Process.* **2**, 97–116.

Olton, D. S. 1979 Mazes, maps, and memory. *Am. Psych.* **34**, 583–596.

Roberts, W. A. 1979 Spatial memory in the rat on a hierarchical maze. *Learn. Motiv.* **10**, 117–140.

Roberts, W. A. 1981 Retroactive inhibition in rat spatial memory. *Anim. Learn. Behav.* **9**, 566–574.

Roberts, W. A. & Dale, R. H. 1981 Rembrance of places lasts: Proactive inhibition and patterns of choice in rat spatial memory. *Learn. Motiv.* **12**, 261–281.

Roberts, W. A. & Smythe, W. E. 1979 Memory for lists of spatial events in the rat. *Learn. Motiv.* **10**, 313–336.

Shettleworth, S. J. & Krebs, J. R. 1982 How marsh tits find their hoards: The roles of site preference and spatial memory. *J. exp. Psychol.: Anim. Behav. Process.* **8**, 354–375.

Walker, J. A. & Olton, D. S. 1979 The role of response and reward in spatial memory. *Learn Motiv.* **10**, 73–84.