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Minireview

The role of stimulus ambiguity and movement in spatial navigation: A multiple memory systems analysis of location discrimination

Norman M. White[*]

Department of Psychology, McGill University, Montreal, QC, Canada H3A 1B1

Abstract

This paper reviews recent findings about how rats navigate by learning to discriminate among locations. The assumption underlying the experiments and their interpretation is that the information required to do this is learned by three independent, parallel memory systems. One system processes cognitive information (or "knowledge"), a second system processes reinforced stimulus–response associations and a third processes Pavlovian conditioned responses in the form of stimulus–affect associations. The information stored in each system produces behavior that, in some cases, results in a location discrimination. The present experiments focus on three factors that influence what each system learns and whether the resulting memory produces behavior that results in a location discrimination. One factor is whether the locations to be discriminated can be identified by unique, unambiguous stimuli or whether they are ambiguously associated with the same stimuli. The second factor is whether the stimuli are observed passively or whether the rats move among them, voluntarily or involuntarily. The third factor is whether or not the rats perform specific reinforced responses in the presence of the stimuli. Instances of co-operative behavioral outputs from memory systems that facilitate location discriminations and of competitive outputs that impede discriminations are described.
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Keywords: Learning; Memory; Multiple memory systems; Hippocampus; Fimbria–fornix; Amygdala; Parallel processing; Conditioned cue preference; Win-stay; Win-shift; 4/8 task

1. Introduction

In the 1940s and 50s experimental psychology was dominated by two main learning theories. "Association" theory, represented primarily by Thorndike (1898, 1933), Hull (1943) and others, asserted that all learning consisted of associations between stimuli and responses. For more complex behaviors, various clever schemes were postulated, including hierarchical patterns of S–R associations and the idea that every learned behavior consists of a very large number of micro-associations between small stimulus elements and small parts of complex response patterns (e.g., Estes, 1959). By definition, S–R associations always include a reinforced response and the response must always be made for it to become associated with a stimulus. When an individual encounters a stimulus situation in which it has previously acquired S–R associations there is no ambiguity about the behavior that occurs. It has been learned as part of those associations.

In contrast, "cognitive" theory, represented primarily by Tolman (Tolman, 1948, 1949; Tolman, Ritchie, & Kalish, 1946), argued that learning involved acquiring information about the relationships among the individual stimulus elements in a situation. These are often called stimulus–stimulus, or S–S, associations. Tolman described such relationships as "expectancies" because S–S relationships constitute information about a situation and the sequence of events that can be expected to occur in it. S–S associations contain no information about behaviors that might or might not be appropriate in the situation. This feature of cognitive theory allowed

[*] Fax: +1-514-398-4896.

E-mail addresses: norman.white@mcgill.ca, nwhite@psych.mcgill.ca.

for flexibility of behavior guided by acquired information about the situation (the S–S associations) and other more immediate factors such as changes in the situation or internal states (Hirsh, 1974). Response specification was a problem for Tolman and remains a problem for cognitive theory up to the present time. Guthrie, an associative theorist, famously criticized Tolman's theory for leaving the rat at the choice point of the maze, "buried in thought" (Guthrie, 1952, p.143).

1.1. S–R vs S–S maze learning

According to association theory, S–R associations are formed automatically when an individual repeatedly makes a consistent response in the presence of a stimulus, and when this sequence is followed by reinforcement. According to cognitive theory, S–S associations are also acquired automatically when an individual is exposed to a novel situation. No particular response or reinforcement are required for the latter process to occur.

This distinction led Thorndike to propose an experiment to test which of the two theories was correct:

> "put the rat in a little wire car, in the entrance chamber of a maze, run it through the correct path ... and into the food compartment. Release it there and let it eat the food morsel provided. (This rat) ... has an opportunity to form expectancies ... that the correct turn is followed by the food ... Compare the behavior of such rats with rats trained in the customary manner (by running through the maze)" (Thorndike, 1946, p. 278).

McNamara, Long, and Wike (1956) did this experiment. They trained hungry rats to find food in a T-maze using two methods. One group ran through the maze normally (voluntary exposure), the other was dragged through it in a small basket (involuntary exposure). Learning was assessed on a series of extinction trials. As can be seen in Fig. 1 when the maze room had normal lighting with a number of visible cues both training methods led to equally good performance. When the same experiment was done with the cues removed and dim lighting the rats that ran through the maze voluntarily learned it normally, but the rats that were moved through the same maze involuntarily failed to learn to find the food.

One way to interpret these findings is that they illustrate two different ways the maze can be learned. In the dark condition (with few visible extra-maze cues) performance of the correct response followed by reinforcement was required for the rats to learn to find the food. This is consistent with S–R learning. However, in the light condition (with plenty of visible extra-maze cues) performance of the response was not necessary. Involuntary movement through the maze environment without performing any specific response was sufficient for the rats to learn to find the food. This is consistent with S–S learning.
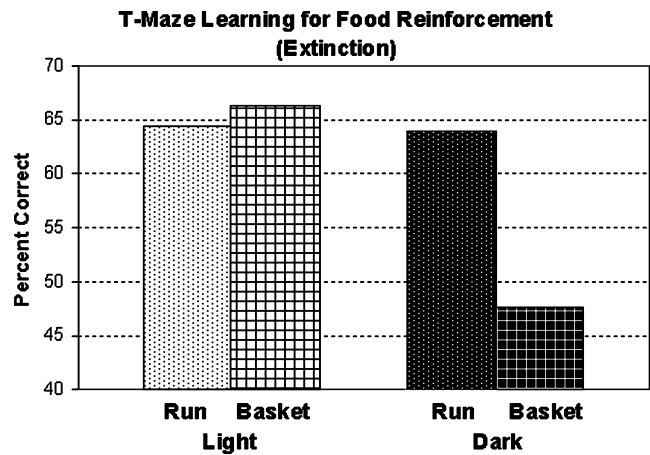

Fig. 1. Rats learned to find food in a T-maze by running through it or by being dragged though it in a basket in two conditions: light, the room was well lit and contained a number of extra-maze cues; dark, the room was dimly lit and all extra-maze cues were removed. The bars show percent correct responses over four extinction trials. In the light condition, learning was good with both training methods; in the dark condition, learning was also good when the rats ran through the maze, but was poor when they were dragged through it. Data from McNamara et al. (1956).

The McNamara et al. experiment suggests that both stimulus and response properties of learning situations interact to determine the nature of the learning that occurs. The presence of sufficient extra-maze cues seems to have permitted a form of learning that does not include information about responses. In the absence of extra-maze cues, the performance of a reinforced response resulted in a form of learning that appears to include information about the response. When the learning situation included both the cues and the reinforced response, it is possible that both forms of learning occurred.

Both types of learning in this experiment involved movement, although of different kinds. As it did not include a condition in which the rats were exposed to the situation without movement, the experiment does not fully address the issue of whether and what kinds of movement are necessary for S–R and S–S learning.

1.2. Parallel types of learning

The idea, suggested by the findings of McNamara et al. that different kinds of learning can occur more-or-less independently and in parallel in the normal brain is the subject of this special issue and the symposium on which it is based. One approach to this issue is a parallel processing model proposed by White and McDonald (2002). These authors suggested that three different kinds of learning can occur simultaneously in the mammalian brain, each in a different neural system. Each of the subcortical systems receives information from the cortex, processes it independently and produces its own behavioral output. A neural system that includes the hippocampus and fimbria–fornix processes S–S learning, a system that includes

the dorso–lateral part of the dorsal striatum (also called caudate nucleus or caudo-putamen in the rat) processes S–R learning. A third system that includes the amygdala processes stimulus–affect (S–Af) learning, to be discussed later. According to the model, each of these neural systems functions independently. They do not communicate learned information directly with each other.

A fundamental feature of any multiple memory system theory is the procedure used to differentiate among types of learning and to attribute each type to a brain system. In the present case, various training procedures are used to give hungry rats different kinds of information about the location of food on an 8-arm radial maze. They are required to discriminate such locations from other specified locations that do not contain food. The maze is rotated by one arm position to the left prior to the start of each daily trial, so information about the maze itself cannot be used to learn the location of the food. The rats must rely on the distal stimuli in the maze environment (in most experiments) to discriminate between the food and no-food locations.

As in the McNamara et al. experiment, the nature of the information about the location of food on the maze provided by different training procedures is determined by the kinds of stimuli that are made available and by the access the rats are given to those stimuli; that is, whether and how they move around on the maze in relation to the stimuli. The interaction between the information provided and the function of different brain systems is studied by impairing the function of the brain systems. When impairment of a brain area leads to impaired discrimination learning with a particular training procedure, the system to which the brain area belongs is assumed to be involved in processing the kinds of information provided by that form of training.

In general, two different kinds of location discriminations on the radial maze are used. The separated arms discrimination uses pairs of arms located on opposite sides of the maze (separated by at least two other arms). When food is placed in one of the arms, the environmental cues indicating its location are unambiguous because almost none of them can be seen from both arms. The adjacent arms discrimination uses pairs of arms located next to each other. In this situation, the cues indicating the location of the food are mostly ambiguous because they can be seen from both the food and no-food arms.

2. Stimulus factors

2.1. Environmental (extra-maze) stimuli in S–S and S–R learning

2.1.1. Win-Shift vs Win-Stay

Packard (1987; Packard, Hirsh, & White, 1989) used an 8-arm radial maze to compare S–S and S–R learning.

The maze was located in a room containing a number of stimuli and the experiment was run with normal room lighting or with the lights dimmed and a plain curtain surrounding the maze to attenuate extra-maze cues.

S–S learning was examined using the standard win-shift task (Olton & Samuelson, 1976) in which rats must obtain a single food pellet from each arm without re-entering empty arms; that is, by avoiding responses that have been reinforced. To do this, the rats must be able to discriminate adjacent arms from each other. They are thought to acquire the required information while moving around on the maze without making any specific, consistent responses, leading to the acquisition of S–S associations in which the stimuli are the extra-maze cues (Rossier & Schenk, 2003; Suzuki, Augerinos, & Black, 1980). These associations are thought to be elaborated into a special form of cognitive map (sometimes called a spatial map, O'Keefe & Nadel, 1978) that includes sufficient information to give each arm a unique label. Correct performance also requires the ability to remember which of the arms no longer contain food as each trial proceeds, a faculty called working memory (Olton, Walker, & Gage, 1978) that also consists of response-free S–S associations. Consistent with this hypothesis about the importance of extra-maze stimuli, Packard found that attenuating those stimuli retarded learning of the win-shift task (Fig. 2A).

In the second task (win-stay learning), the location of food was indicated by small lights at the entrance to 4 of the 8 arms of the maze. A randomly selected pattern of 4 different arms was lit and contained food on each daily trial and the dark arms were always empty. The rats received reinforcement every time they entered a lit arm—the conditions for S–R learning. Normal rats trained in the attenuated cue condition learned to find food faster than rats trained in the normal cue condition (Fig. 2B). The opposite effects of the extra-maze cues on the win-shift and win-stay tasks suggests that they were learned in different ways.

This idea was supported by the observations (Packard, 1987; Packard et al., 1989) that lesions of the dorsal striatum impaired win-stay but not win-shift learning and lesions of the fimbria–fornix impaired win-shift but not win-stay learning (Fig. 2), suggesting that the fimbria–fornix is required for normal S–S learning (spatial learning in this case), and that the dorsal striatum is required for normal S–R learning. There is considerable evidence that similar fimbria–fornix lesions impair spatial learning in a variety of situations (O'Keefe, Nadel, Keightley, & Kill, 1975; Olton & Samuelson, 1976; Olton et al., 1978; Sutherland & Rodriguez, 1989; Wible, Shiber, & Olton, 1992), and that lesions of the dorsal striatum impair other forms of S–R learning (Packard & Knowlton, 2002; White, 1997).

It is interesting to note that the rats with dorsal striatum lesions did not acquire win-stay behavior even
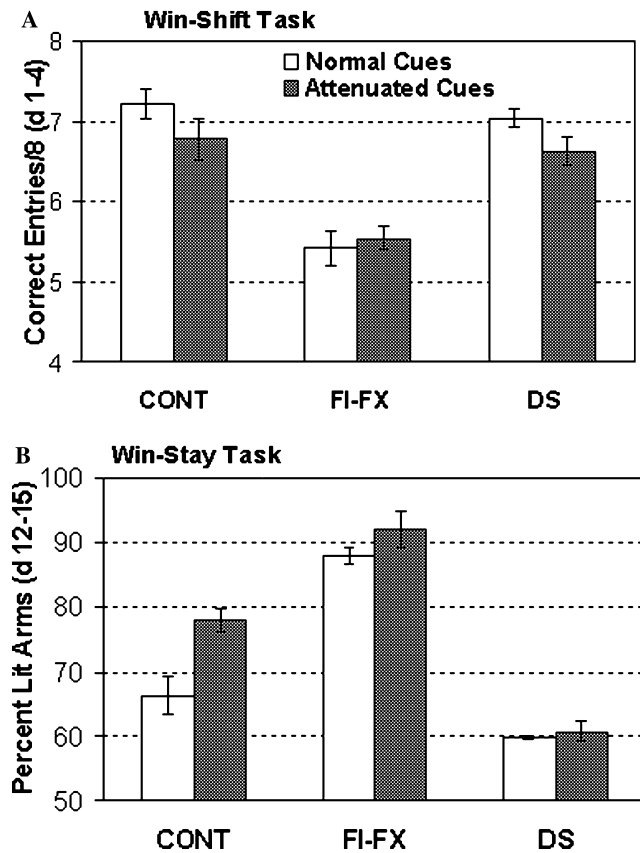
Fig. 2. (A) Performance on win-shift task (see text for details) with normal and attenuated (curtain surrounding maze, lights dimmed) extra-maze cues. Bars show mean correct arm entries (first entries to each arm) over 4 daily trials (±SEM). Performance was facilitated by the presence of extra-maze cues, impaired by fimbria–fornix lesions and unaffected by dorsal striatum lesions. (B) Performance on win-stay task (see text for details) with normal and attenuated extra-maze cues. Bars show mean percent correct arm entries (to lit arms) over last 4 days of testing. Performance was impaired by the presence of extra-maze cues, impaired by dorsal striatum lesions and facilitated by fimbria–fornix lesions. Data from Packard (1987).

though their fimbria–fornix and hippocampus were functional, as indicated by their ability to learn the win-shift task normally.

2.1.2. The 4/8 task

In this task rats are placed on the maze with food in the same 4 arms on every trial; The other 4 arms are always empty. No intra-maze cues indicate the locations of the food. Using extra-maze cues only, rats must learn to avoid arms that do not contain food and to enter each of the food arms once only.

Packard (1987; Packard & White, 1990) studied the effects of fimbria–fornix and dorsal striatum lesions on the performance of this task (Fig. 3). As shown in Fig. 3A, lesions of both structures initially impaired learning to avoid the no-food arms, but both lesion groups showed some evidence of learning with sufficient training. This pattern of effects suggests that the task was learned in two
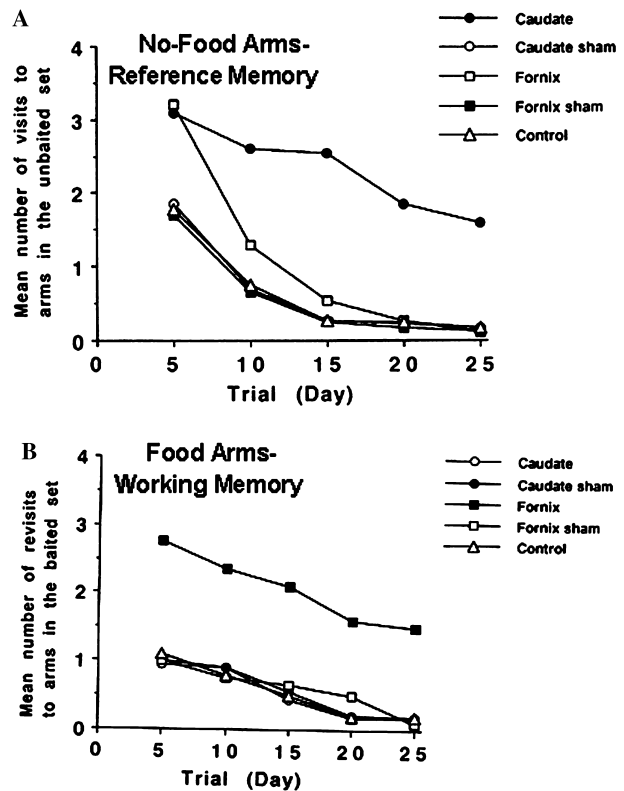

Fig. 3. Performance on the 4/8 task. Food was consistently available on the same four radial maze arms over 25 daily trials, shown in five trial blocks. (A) Errors in avoiding no-food arms (unbaited set). Rats with either fimbria–fornix or dorsal striatum (Caudate) lesions were initially impaired compared to normal and sham control groups. Both lesion groups showed some evidence of learning with additional training. (B) Errors in entering each food arm (baited set) once only. Rats with fimbria–fornix lesions were impaired compared to rats with dorsal striatum (Caudate) lesions and control groups. Data from Packard (1990).

different ways. Since the extra-maze cues visible from the food arms were the same on every trial, tendencies to enter some of the food arms could have been acquired as reinforced S–R associations, impaired by dorsal striatum (caudate nucleus) lesions. The locations of food in the maze environment could also have been learned as features in an S–S-based spatial map, a form of learning impaired by fimbria–fornix lesions.

This analysis suggests that the tendency of the rats with fimbria–fornix lesions to enter the food arms was based on dorsal striatum—mediated S–R associations, and that the tendency of the rats with dorsal striatum lesions to enter the food arms was based on a fimbria–fornix—mediated spatial map of the maze environment. A comparison of the learning rates in the two lesion groups suggests that the S–R system acquired a type of information that produced this discrimination more quickly than the S–S system. However, in normal rats both forms of learning contributed to learning to avoid the no-food arms, an instance of co-operative output from two independent learning systems.

The findings also show that dorsal striatum—mediated S–R learning can occur with distal cues as the stimuli and that this form of learning is not limited to the kinds of local cues used in the win-stay task already described.

Fig. 3B shows that fimbria–fornix lesions impaired the second part of the 4/8 task: entering each of the food arms once only. The working memory required for this behavior is the same as for the win-shift task and both are impaired by the same lesions.

2.2. Ambiguous and unambiguous discriminations

In the 4/8 experiment just described, the food arms were chosen randomly for each rat. Some of them were adjacent to each other and some were separated from each other by no-food arms. As already described, this means that the stimuli available to discriminate between any pair of food and no-food arms were ambiguous in some cases and unambiguous in others. McDonald and White (1995b) examined the kinds of learning produced by exposure to ambiguous and unambiguous cues and the neural structures that mediate them by training rats to find food on a radial maze in a series of discrete trials. On each trial, the rat was placed on the center platform and offered a choice between two arms. The same arm contained piece of food on all trials, the other arm was always empty. In different experiments, the empty arm was adjacent to or separated from the food arm and was located either to the right or left of the food arm on equal numbers of counterbalanced trials. Each trial terminated when the rat ran to the end of an arm, regardless of whether or not it contained food. With 10 trials per day normal rats learned to discriminate between both separated and adjacent arms within a few days.

2.2.1. Separated arms

Learning the separated arms discrimination with this form of training was unaffected by lesions of the fimbria–fornix, amygdala or dorsal striatum. A possible explanation for this finding is that this unambiguous discrimination was learned in more than one way, as in learning to avoid the no-food arms in the 4/8 task. The rats could have acquired a fimbria–fornix—mediated spatial map of the environment that included information about the location of the food. At the same time, the rats repeatedly entered an arm and found food. Since the food was always in the same arm the cues visible from that arm remained constant, and since the no-food arms were on the opposite side of the maze the cues were also unambiguous. This could have resulted in S–R learning.

The hypothesis that the rats could learn the active separated arms discrimination in two different ways, each with a different memory system, explains the finding that lesions of either system had no effect on per-formance of the task The hypothesis predicts that rats with lesions of both fimbria–fornix and dorsal striatum should be impaired on this task and this result was obtained in the experiment (McDonald & White, 1995b). Neither combined amygdala and fimbria–fornix lesions nor amygdala and dorsal striatum lesions affected performance. This finding is consistent with the suggestion that behavior produced by two independent forms of learning, a reinforced S–R association and information about the location of food in a spatial map of the maze environment, results in a discrimination between locations defined by separated arms.

2.2.2. Adjacent arms

Learning the adjacent arms discrimination with discrete trials was impaired by fimbria–fornix lesions and unaffected by lesions of either the amygdala or dorsal striatum (McDonald & White, 1995b). This is consistent with findings already described showing that rats can learn to discriminate among locations defined by ambiguous cues when they move around on the maze, and that this kind of learning requires an intact fimbria–fornix. The finding is also consistent with a report that hippocampus lesions result in a similar inability to discriminate between closely spaced but not widely spaced locations (Gilbert, Kesner, & DeCoteau, 1998).

Rats with fimbria–fornix lesions and normal dorsal striatums were unable to learn the active adjacent arm discrimination even though they experienced the same sequence of repeatedly entering a consistent arm containing food as did the rats trained on the active separated arms discrimination. The use of this form of training suggests that the same form of S–R learning must have occurred in both situations, but that it was unable to produce the required discrimination with adjacent arms. This may be because S–R associations consist of individual stimuli and responses. If an association is formed between the stimuli visible from an arm and the response of entering the arm, and if most of the same stimuli are visible from an adjacent arm, the association should produce a nearly equal tendency to enter both arms. This means that the behavior produced by an S–R association cannot discriminate between locations defined by adjacent arms.

2.3. Summary

In the experiments discussed, rats moved around on the maze voluntarily and were required to discriminate between locations defined by ambiguous or unambiguous cues. The findings suggest that discriminations between locations defined by unambiguous cues can be produced by S–R associations if two conditions are met. The stimuli visible from the location must remain constant and the response must be reinforced (nearly) every time it is made. S–R learning was consistently impaired

by lesions of the dorsal striatum, but unaffected by lesions of the fimbria–fornix.

The behavior produced by S–R associations failed to discriminate among locations that could only be identified by ambiguous stimuli. This does not mean that this form of learning did not occur in these situations, but that the associations acquired did not produce the discrimination. The possibility remains that S–R associations could produce ambiguous cue discriminations with much larger numbers of training trials than were given in the experiments described. If this were the case, it would not affect the conclusion that S–R learning does not normally contribute to making such discriminations in most situations.

The evidence shows that ambiguous cue discriminations are learned without specifying any specific responses, suggesting that they consist of S–S associations, aggregations of which constitute cognitive or spatial maps. Ambiguous locations are discriminated by their relationships to multiple stimuli within these maps, a process sometimes called "pattern separation" (Kesner, Gilbert, & Wallenstein, 2000; Maar, 1971; Mizumori, Ragozzino, Cooper, & Leutgeb, 1999; Rolls, 1996). In the experiments described here, S–S learning was consistently impaired by lesions of the fimbria–fornix, a major input–output pathway of the hippocampus. Similar results have been reported for hippocampal lesions (Gilbert et al., 1998; Kesner, Gilbert, & Barua, 2002) and, more specifically, for lesions of the dentate gyrus (Gilbert, Kesner, & Lee, 2001).

The behavior of rats with dorsal striatum lesions in both the win-stay and 4/8 tasks suggests that fimbria–fornix—mediated S–S learning results in poor discrimination between unambiguous cues. However, the fact that both fimbria–fornix and dorsal striatum lesions were required to impair the separated arms discrimination in the discrete trial task shows that this is not always the case. Further investigation of the conditions under which S–S learning can produce unambiguous cue discriminations is required.

On the basis of the evidence discussed so far, the training that produced both ambiguous and unambiguous discriminations based on either S–R or S–S learning involved movement, although of different kinds. S–R learning requires that a specific response be made, and that response is acquired as part of the association that is learned. All instances of S–S learning described have also involved movement, although this required no specific responses and did not have to be voluntary, as shown by McNamara et al.

Even though they can be learned with forms of training that involve movement, the question remains if movement is required to discriminate between ambiguous or unambiguous locations. Can either or both of these discriminations be produced by a form of learning that does not require movement?

3. The role of movement in discrimination learning

One way to examine the contribution of movement to these forms of learning is to feed rats while they are confined on the end of an arm. Since they cannot move around on the maze and do not make any specific reinforced responses, failure to learn the location of the food with this form of training would suggest that movement is essential for the rats to learn to discriminate among the locations defined by the arms available to them on the test.

This procedure is called the conditioned cue preference (CCP) task. On alternate days rats eat while confined on the end of one arm of the maze with a supply of food and spend an equal amount of time on the end of another arm with no food. After several such training trials, they are placed on the center platform of the maze and allowed to move freely between the two arms, neither of which contains food. Rats that spend more time on the food-paired arm than on the no-food (unpaired) arm are taken to have learned the location of the food, which requires them to discriminate between the locations defined by the two arms.

When the food-paired and unpaired arms are separated by at least two other arms normal rats learn the CCP with one or two training trials (White & McDonald, 1993). However, when the food-paired and unpaired arms are adjacent to each other normal rats show no evidence of learning the discrimination after as many as eight training trials (Chai & White, 2004; McDonald & White, 1995b). The findings suggest that movement is not required to learn the separate arms CCP but that it is required to learn the adjacent arms CCP.

3.1. Separate arms discrimination

The fact that rats were able to learn the separate arms CCP without making any specific reinforced response violates the principles of S–R learning. Instead, the rats ate in the presence of stimuli visible from the food-paired arm and spent an equal amount of time in the presence of a different set of stimuli visible from the unpaired arm.

This learning situation can be modeled as an instance of classical or Pavlovian conditioning (Pavlov, 1927). The food on the paired arm is the US, which is assumed to elicit some positive internal affective response, the UR. The stimuli visible from the paired arm (the CS) become associated with the US and/or the UR and elicit the CR, or conditioned affective response. No such associations are formed with the cues visible from the unpaired arm. When the foraging rats enter the food-paired arm (now empty) during testing the CS elicits the CR causing the rats to spend more time exploring that arm than the unpaired arm. Thus, when the CCP procedure is used, the separated arm discrimination could

be due to Pavlovian conditioning. The acquired information in this case can be described as a stimulus–affect (S–Af) learning.

Many forms of appetitive Pavlovian conditioning are impaired by lesions of the amygdala (Everitt, Morris, O'Brien, & Robbins, 1991; Jones & Mishkin, 1972; Kesner, Walser, & Winzenried, 1989; Weiskrantz, 1956), and the same is true for separate arm CCP learning (White & McDonald, 1993). Similar lesions have no effect on win-stay learning (McDonald & White, 1993). Lesions of the dorsal striatum similar to those that impair win-stay learning have no effect on separate arms CCP learning (White & McDonald, 1993).

These findings suggest that the separate arms CCP and win-stay training procedures result in different kinds of learning mediated at least in part by different brain areas. Learning to discriminate between separated radial maze arms by a acquiring a reinforced response is attributable to S–R learning mediated in part by the dorsal striatum. When rats learn the same discrimination without making any specific reinforced response the discrimination is attributable to amygdala-mediated S–Af learning.

3.2. Adjacent arms discrimination

In contrast to the ease with which normal rats learn to discriminate among adjacent radial maze arms when they move around on the maze (McDonald & White, 1993; McDonald & White, 1995b; Packard & White, 1990), this form of learning is severely retarded when the rats' only exposure to the environment occurs while they are confined to the ends of the maze arms (Chai & White, 2004). This suggests that movement may be required to discriminate among locations that can only be defined by ambiguous stimuli.

However, this movement requirement is different from that for S–R learning. This was shown clearly in an experiment (Chai & White, 2004) in which rats were allowed to explore the maze voluntarily with no food available ("pre-exposure") before CCP training. A minimum of three daily 10 min pre-exposure sessions followed by four training trials produced an adjacent arms CCP (Fig. 4A). A similar amount of pre-exposure to a maze in a different room did not have this effect. Thus, voluntary, unreinforced exploration of the environment prior to training provided sufficient information for the rats to discriminate between adjacent arms.

This demonstration of latent learning (Blodgett, 1929; Tolman & Honzik, 1930) suggests that during the pre-exposure sessions rats acquire information specific to the maze environment: the S–S associations making up the spatial map. This kind of information cannot be acquired during the training trials because this requires movement and the rats are confined in the ends of the
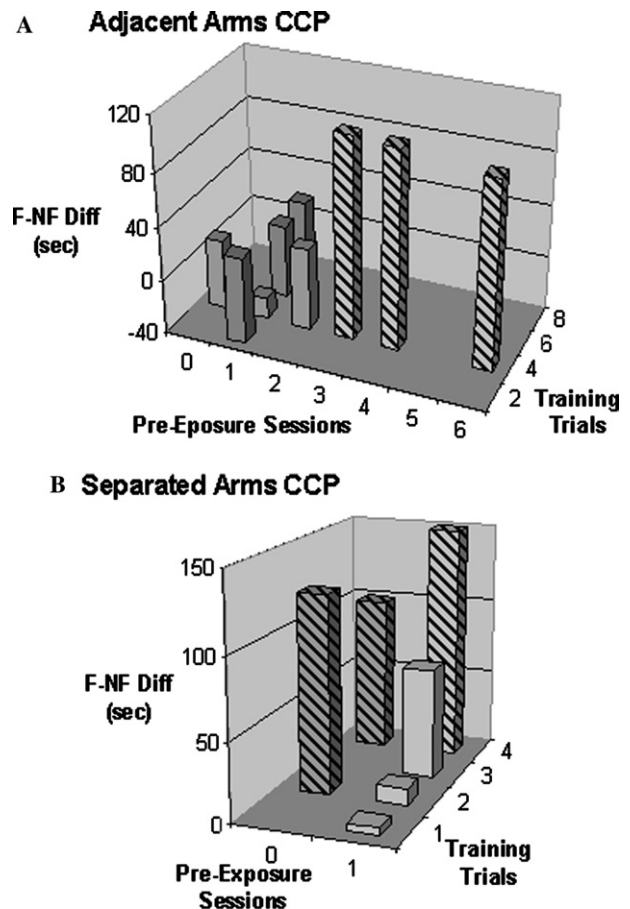

Fig. 4. Effects of unreinforced pre-exposure and training on adjacent and separate arm CCP learning on a radial maze. Rats received 0–6 daily 10 min sessions of Pre-Exposure (exploring the maze with no food available) followed by 1–8 Training Trials (each consisting of 30 min of confinement on the end of one arm with food and on the end of another arm with no-food) followed by a test (rats given a choice between the food and no-food arms, neither of which contains food). Bars show the difference in time spent on the two arms (F-NF Diff). Cross-hatched bars indicate significant preferences. (A) Pre-Exposure facilitates adjacent arms CCP learning. After 1 Pre-Exposure session rats failed to learn the CCP with up to 8 Training Trials. After a minimum of 3 Pre-Exposures they learned the CCP with 4 Training Trials. Data from McDonald and White (1995b), Chai and White (2004). (B) Pre-Exposure retards separated arms CCP learning. With no Pre-Exposure sessions rats learned the separated arms CCP with 2 Training Trials. After 1 Pre-Exposure they required a minimum of 4 Training Trials. Data from McDonald and White (1995a), White and Ouellet (1997).

arms. However, it appears that the information acquired during pre-exposure can be used during the training trials to learn the location of the food in the maze environment with sufficient accuracy to discriminate between adjacent arms.

The idea that spatial information is acquired during the unreinforced pre-exposure sessions is consistent with the observation that lesions of the fimbria–fornix eliminated the latent learning effect when made before, but not after pre-exposure (Chai & White, 2004).

4. "Pure" spatial learning

The observation that pre-exposure in a different environment does not facilitate adjacent arm CCP learning shows that information specific to the maze environment is learned during these sessions. This information may be purely spatial. It does not include information about responses, either of the reinforced type that are part of S–R associations, or of the affective type that are part of S–Af associations. Hence, the term "pure spatial learning."

The same pre-exposure manipulation also affects the separated arms CCP, although in the opposite direction (Fig. 4B). The separated arms CCP is learned with two training trials; a single 10 min pre-exposure session increases the minimum number of trials to four (McDonald & White, 1995a). Unreinforced pre-exposure to the CS is known to retard subsequent conditioning in a variety of Pavlovian conditioning paradigms (Chacto & Lubow, 1967; Chamizo & Mackintosh, 1989; Solomon & Moore, 1975; Weiner & Feldon, 1987), a phenomenon called latent inhibition (Lubow, 1973).

Latent inhibition of the separated arms CCP is impaired by fimbria–fornix lesions made before but not after the pre-exposure session (McDonald & White, 1995a), the same pattern of effects as with latent learning in the adjacent arms situation, suggesting the possibility that the same kind of information acquired during pre-exposure produces both effects. This suggestion will require further investigation.

4.1. Hippocampal function in pure spatial learning

It has been suggested that the information acquired during pre-exposure consists of a spatial map of the maze environment in the form of S–S associations, and that acquisition of this information requires an intact fimbria–fornix. The other brain structure usually associated with this type of learning is the hippocampus (Eichenbaum, Stewart, & Morris, 1990; Jarrard, 1986; Morris, Garrud, Rawlins, & O'Keefe, 1982; O'Keefe & Nadel, 1978; Olton et al., 1978), leading to the prediction that lesions of this structure should eliminate both the latent learning and latent inhibition effects of unreinforced pre-exposure. However, there is at least one early experiment (Kimble & BreMiller, 1981) showing clearly that hippocampus lesions do not affect latent learning of a maze. In our experiments with the adjacent arms paradigm, hippocampus lesions made before or after pre-exposure eliminated CCP learning (Chai & White, 2004). Because of the possibility that the hippocampus is required for learning or expression of this CCP task, these effects could not necessarily be attributed to impaired latent learning. However, temporary inactivation of the hippocampus with muscimol before the pre-exposure sessions did not impair adjacent arms CCP learning (Gaskin & White, unpublished observations). The same treatment in the same rats impaired win-shift performance. This means that a functional hippocampus was not required for the latent learning effect in the adjacent arms paradigm.

Similarly, large neurotoxic lesions of the hippocampus made before pre-exposure had no effect on latent inhibition of the separated arms CCP (White & Wallet, 2000). The hippocampal rats that failed to show impaired latent inhibition were subsequently tested and found to be impaired on win-shift learning, showing that the lesions were effective. The fact that the separate arms CCP is an amygdala-based task allowed examination of the effects of hippocampus lesions on pre-exposure without interfering with acquisition of the CCP itself.

Taking the latent learning and inhibition findings together suggests that an intact fimbria–fornix is required for the acquisition but not expression of the information acquired during voluntary, unreinforced exploration, but that the hippocampus is not involved in acquisition of the same information. The hippocampus is, however, required for retrieval and/or expression of the information required to perform the adjacent arms discrimination.

4.2. Spatial learning vs learning the location of food

During normal maze learning, as in the active adjacent arms procedure, rats learn the location of food in a spatial map. The CCP procedure separates this learning situation into two components. During pre-exposure, the rats acquire pure spatial information but learn nothing about the location of the food because there is no food on the maze. Food is present in one arm during training but the rats cannot acquire any spatial information during these trials because they cannot move around on the maze. The idea that these are different learning processes is consistent with the findings that acquisition of the spatial information but not acquisition of the information about the food was impaired by fimbria–fornix lesions. In contrast, inactivation of the hippocampus had no effect on acquisition of the pure spatial information, but hippocampus lesions did affect acquisition and/or expression of information about the location of the food.

As shown by the discrete trial experiments, these two forms of learning normally occur simultaneously. Taken together, the present findings suggest that during active maze learning fimbria–fornix mediates pure spatial learning and hippocampus mediates the addition of information about the food to the spatial map. Hippocampus may also mediate recall and expression of the combined information to produce behavior that results in the location discrimination.

5. Voluntary vs involuntary movement

The latent learning and inhibition effects discussed so far were produced by voluntary, unreinforced exploration, and it has been suggested that both effects may be due to the acquisition of a series of S–S associations that form some kind of spatial map. Evidence discussed argues for a distinction between this form of learning and S–R learning, in which specific responses are reinforced, and S–Af learning, which involves responses elicited by reinforcers.

However, it has been pointed out that when rats explore an environment they necessarily make responses, and some forms of learning could be based on sensory or motor feedback ("ideothetic" information) from these responses. Among others, these processes could include proprioceptive learning (Potegal, 1987) and path integration (Etienne, Maurer, & Séguinot, 1996; Maaswinkel & Whishaw, 1999; Whishaw, 1998; Whishaw & Brooks, 1999). The issue of whether any form of responding is necessary to acquire the information required to produce the latent effects was examined in two series of experiments.

5.1. CCP learning

First, the possibility of CCP learning with involuntary movement was examined (White & Ouellet, 1997). To produce involuntary movement rats were confined in the ends of two maze arms (either separated or adjacent) for 5 min periods and switched back and forth between them by the experimenter. One arm contained food, the other was empty, and the rats spent a total of 15 min in each arm on each of 4 days. The rats in an unswitched control group were picked up by the experimenter an equal number of times and always returned to the same arm; either the food or no food arm on alternate days.

5.1.1. Adjacent arms
Rats trained in the switched condition acquired the adjacent arms CCP, but rats trained in the unswitched condition did not acquire it (White & Ouellet, 1997). This shows that movement, but not voluntary movement is required to discriminate between locations defined by ambiguous cues. Moreover, since the rats in this experiment had never been on the center platform of the maze prior to the test trial, the result also shows that movement along a trajectory of any kind is not necessary to learn this discrimination. Rather, the result is consistent with the idea that the rats acquired information about the spatial location of food by being exposed to the stimuli in the maze environment from two different locations within a short period of time. These two views may have provided the information required to compute a spatial map. The findings also suggest that the main function of voluntary exploration is to provide

views of the environmental stimuli from different locations. The nature of the movement itself and whether it is initiated by the rat or by an obliging experimenter seems irrelevant.

The idea that the information acquired by the switched group was spatial is consistent with the finding that the CCP learned in this condition was eliminated by fimbria–fornix but not by amygdala lesions, both made before the start of training (White & Ouellet, 1997).

5.1.2. Separated arms
Normal rats learned the separated arms CCP in both the switched and unswitched conditions. The CCP in the unswitched condition was probably due to amygdala-based S–Af learning (i.e., a Pavlovian conditioned response to cues visible from the food-paired arm) because, except that the rats were picked up briefly five times during each session, the unswitched condition was essentially a replication of the standard separated arms procedure.

The separated arms CCP in the switched condition could have been due to acquisition of the same S–Af associations, since the rats trained in that condition spent the same total time on their food paired arms as the unswitched rats, and this discrimination should have been impaired by amygdala lesions. However, rats trained in the switched condition should also have learned the spatial location of the food, as did the rats in the adjacent arms switched condition. Expression of this form of learning would have produced the same discrimination, and should have been impaired by fimbria–fornix lesions. The hypothesis that the same separated arms discrimination was learned in two different ways by two different memory systems leads to the prediction that lesions to either of the two systems would have no effect on the discrimination because the other system would remain intact and able to produce an appropriate behavior. This prediction was confirmed in the experiment (White & Ouellet, 1997).

The hypothesis also predicts that impairing both systems simultaneously would eliminate the discrimination, as was the case for the effect of combined dorsal striatum and fimbria–fornix lesions on the active separated arms discrimination. Unfortunately, this part of the hypothesis was not tested.

5.2. Pre-exposure

The role of movement in the latent inhibition effect has also been examined using the switching procedure during pre-exposure (White, Holahan, & Goffaux, 2003). Rats switched between maze arms with no food in either one exhibited latent inhibition of subsequent separated arms CCP learning. Rats given the same form of pre-exposure to a maze in a different room did not exhibit latent inhibition. These findings suggest that the

information acquired during pre-exposure depends on viewing the specific stimuli that will subsequently become associated with the food from two different locations, and not on any specific movements or responses that may be made during voluntary pre-exposure.

The latent inhibition effect produced by involuntary, unreinforced pre-exposure to the maze environment was impaired by fimbria–fornix lesions made before, but not after pre-exposure and was unaffected by large neurotoxic lesions of the hippocampus made before pre-exposure (White et al., 2003). These lesion findings parallel those for voluntary exploration and are consistent with the idea that both forms of pre-exposure produced the same form of learning, resulting in the latent inhibition effect. The possibility that involuntary pre-exposure to the maze environment may produce latent learning has not yet been tested.

5.3. Working memory

It is generally agreed that several of the learning tasks discussed here, such as remembering which arms have been visited during each trial on the win-shift and 4/8 tasks, require working memory (Honig, 1978; Laroche, Davis, & Jay, 2000; Moore, 1979; Nadel & MacDonald, 1980; Olton & Papas, 1979). These tasks and others involving ambiguous cue discriminations also require spatial learning to identify individual locations in relation to the overlapping stimuli visible from each arm.

The findings of the switching experiments suggest that spatial learning occurs when rats are exposed to more than one location in an environment within the same 30 min session, but does not occur when the rats are exposed to the same two locations 24 h apart. This difference can be explained by the hypothesis that a neural representation of the environmental cues is acquired from the first location and that this representation has a limited duration. A spatial map can be computed only if a representation of the same cues from another location is acquired before the first representation decays. On this hypothesis, acquiring a spatial map depends on a form of working memory.

The hypothesis that spatial learning requires working memory is consistent with the finding that fimbria–fornix lesions impair performance on tasks that require working memory and on those that require spatial learning.

6. Parallel processing

One of the assumptions of the present analysis of spatial navigation is that several different kinds of learning occur simultaneously, each in a different neural system. Depending on how each system processes the information in any given learning situation their outputs may lead to co-operating or competing behaviors (White & McDonald, 2002). In the active separated arms discrimination both fimbria–fornix/hippocampus—mediated S–S learning and dorsal striatum-based S–R learning produced behaviors that discriminated between the locations defined by the two maze arms. In the 4/8 task, the same two systems may have contributed to discriminating between the food and no-food arms. These instances of co-operation between systems occurred because the behavioral outputs of the systems resulted in similar location discriminations.

It is also possible for the outputs of two systems to compete with each other by promoting different behaviors (Hirsh & Krajden, 1982). The notion of competition among the outputs of memory systems predicts that, in some cases, impairments of one system will improve performance by eliminating a behavior that competes with the one defined as correct in the particular test being used. This kind of demonstration is strong evidence for the idea that the systems process information independently of each other.

Among a number of examples of this phenomenon, rats with hippocampal lesions performed better than normals on two-way active avoidance (Isaacson & Douglas, 1961) and rats with fimbria–fornix lesions performed better than normals on a simple olfactory discrimination problem (Eichenbaum, Fagan, Matthews, & Cohen, 1988). Rats with fimbria–fornix lesions also perform better than normals on the win-stay radial maze task (Fig. 2) (McDonald & White, 1993; Packard et al., 1989). In these cases, fimbria–fornix lesions eliminated erroneous responding to distal cues, allowing expression of the correct dorsal striatum—mediated S–R responses without interference (Packard, 1990). In an experiment using a water maze (McDonald & White, 1994), rats were trained to locate a hidden platform using spatial information based on distal cues and to swim directly to the platform when it was visible. When given a choice between these two alternatives (in different locations) rats with fimbria–fornix lesions swam to the visible platform but rats with dorsal striatum lesions swam to the spatial location of the hidden platform (McDonald & White, 1994). In another task involving competition between cue and place learning in a T-maze, Packard and McGaugh (1996) showed that hippocampus-based spatial learning occurs faster than dorsal striatum-based S–R learning but that even after the rats switch to performing responses based on the latter the hippocampus-based memory is still available to control behavior when dorsal striatum function is impaired. These findings are evidence for independent, parallel processing of information by neural systems that include either the fimbria–fornix and hippocampus, or the dorsal striatum.

Recently, Chai and White (2004) demonstrated a similar form of competition between amygdala—medi-

ated and fimbria–fornix/hippocampus—mediated learning using the adjacent arms CCP task. Normal rats learned this discrimination with a minimum of three sessions of unreinforced pre-exposure followed by four training trials (Fig. 4); however, rats with amygdala lesions learned it after only a single session of pre-exposure (Fig. 5). Rats with amygdala lesions that were not pre-exposed or that were pre-exposed to a maze in a different room failed to learn the discrimination. Rats with both amygdala and fimbria–fornix lesions given a single pre-exposure also failed to learn (Fig. 5). It therefore appears that normal rats acquire sufficient pure spatial information in a single pre-exposure session to learn the adjacent arms discrimination, but that some form of simultaneously acquired amygdala-based learning interferes with its expression.

Except for the relative locations of the food-paired and unpaired arms, the procedures in the adjacent and separated arms CCP tasks are identical. Therefore, if rats acquire an amygdala-based CCP in the separated arms task they should also acquire one in the adjacent arms task. Since the cues visible from the paired arm are unambiguous in the separated arms task this form of learning is sufficient to produce a discrimination. However, when the cues visible from the paired arm are ambiguous as in the adjacent arms task, amygdala-based learning does not produce a discrimination between the two arms. In this situation, S–Af learning may produce an equal tendency to enter both arms. To test this hypothesis, normal rats were trained on a three-arm

task, with a food-paired arm and two no-food arms, one adjacent to and one separated from the food-arm. On the test day the rats were given a choice between the two no-food arms. They showed a strong preference for the arm adjacent to the food arm, and this preference was eliminated by lesions of the amygdala (Chai & White, 2004).

These findings suggest that two different forms of learning occur in normal rats during adjacent arms CCP training. A hippocampus-based system combines previously learned spatial information about the maze environment with new information about the location of food in that environment. This information produces the adjacent arms discrimination during the test trial. At the same time, an amygdala-based system acquires a conditioned approach response that does not discriminate between the adjacent food and no-food arms, producing an equal tendency to enter both during the test trial. In normal rats that have received one session of pre-exposure, this behavior interferes with expression of the preference for the food arm produced by output from the hippocampus system. Impairment of the amygdala eliminates this interfering behavior, allowing expression of the hippocampus-based discrimination.

As already described (Fig. 4), the amygdala-based separate arms CCP is subjected to latent inhibition by unreinforced pre-exposure to the conditioned cues. This may be why the adjacent arms discrimination is observed in normal rats that have had sufficient pre-exposure to the maze (three sessions in our experiments). This amount of pre-exposure may produce sufficient latent inhibition of the interfering amygdala-based response to permit expression of the hippocampus-based discrimination.
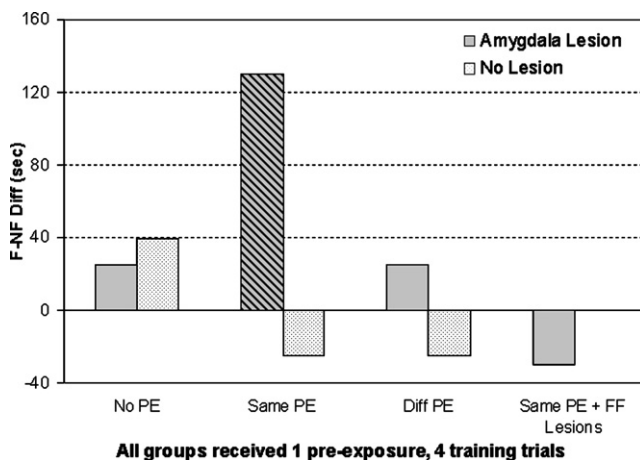

Fig. 5. Adjacent arm CCP learning by rats given 1 Pre-Exposure session and 4 Training Trials. See Fig. 4 and text for procedural details. Bars show the difference in time spent on the two arms (F-NF Diff). Cross-hatched bar indicates significant preference. Rats with amygdala lesions pre-exposed in the same room (Same PE) acquired the the discrimination. Rats with amygdala lesions not pre-exposed (No PE) or pre-exposed in a different room (Diff PE) failed to acquire the discrimination, as did normal (No Lesion) rats in all pre-exposure conditions. Rats with combined amygdala and fimbria–fornix lesions did not learn the CCP (Same PE + FF Lesions). Data from Chai and White (2004).

7. Summary

An expanded parallel processing model is shown in Fig. 6. As in the original model (White & McDonald, 2002), its central feature is three independent parallel neural systems, each of which receives information from cerebral cortex, processes it in a unique way, and produces its own behavioral output. Several instances of co-operative and competitive output have been described.

The dorsal striatum system processes S–R associations These associations are acquired when consistent responses to specific stimuli are reinforced. Since a stimulus can only be associated with one response, the behavior produced by dorsal-striatum—mediated S–R associations result in discriminations among unambiguous, but not among ambiguous cues.

The amygdala system processes S–Af (or Pavlovian) associations. These are acquired when a reinforcer is encountered in the presence of otherwise neutral stimuli. The stimuli acquire the ability to elicit affective
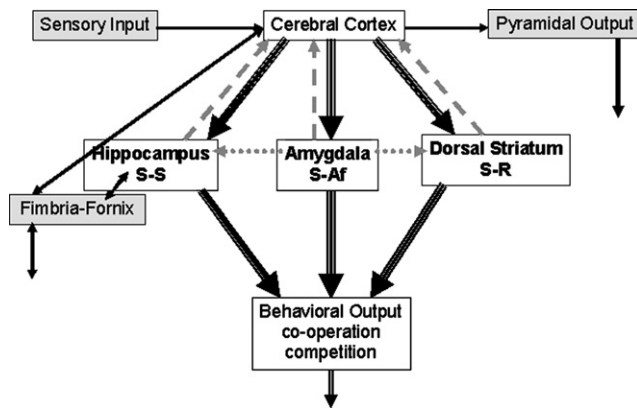
Fig. 6. Expanded parallel processing model. Three parallel systems for memory/information processing are indicated by heavy double-lined arrows. Each system is defined by a central structure (bold type) labeled with the type of information it processes (see text for details). Each of the three systems receives information from the cortex, processes it in its unique way and produces its own influence on behavior. As indicated on the figure, these processes occur completely independently except for amygdala-mediated memory modulation (light grey dotted arrows) which does not involve transmission of the information being processed by any of the structures. Output from each of the memory systems is known to influence the cortex (light dashed arrows), leading to the as yet unproven suggestion that any one of these influences could change the nature of the information represented there and sent to all three of the systems. This would constitute an indirect form of communication among the systems. Sensory input to the cortex and its own pyramidal tract output also presumably influence behavior. Evidence is presented in the text for the involvement of the fimbria–fornix (but not the hippocampus) in the acquisition of pure sensory information.

responses similar to those produced by the reinforcer. S–Af associations do not include any kind of learned behavior. However, conditioned affective responses can result in increased contact with conditioned stimuli that elicit them, causing rats to approach and spend more time in locations where they are active. Because they do not include any spatial information, amygdala—mediated S–Af associations can produce behavior that results only in unambiguous cue discriminations.

The hippocampus system (including the fimbria–fornix) appears to mediate true spatial learning, in the sense that it is capable of locating cues with respect to other cues in the environment. This flexibility means that the S–S associations it is thought to process are the only form of learning that can discriminate locations defined by ambiguous cues. This ability may actually consist of two distinguishable types of learning. One is the acquisition of pure spatial information mediated by the fimbria–fornix, but not by the hippocampus. Movement, but not necessarily voluntary movement is required for this type of learning. Movement appears to provide views of the environmental stimuli from different locations. Because these views cannot be obtained at the same time, a form of working memory is required to keep the neural representations of each one active until

sufficient views have accumulated to enable computation of the spatial map.

Given its anatomical connections, it seems unlikely that the fimbria–fornix carries the spatial information used to compute the spatial map. It is more likely that it carries a signal that facilitates the computation of a spatial map using sensory information arriving in the cortex via its afferent pathways. It should also be noted that other forms of information, such as sensory and motor feedback, can also be used in spatial navigation; however, the present findings suggest that S–S learning is used preferentially, when the required stimulus information is available.

The data suggest that spatial information acquired in this way does not include information about reinforcers or other salient events. Learning about the presence of reinforcers or the occurrence of other events within the spatial map is the second type required for discriminating ambiguous locations. Both the acquisition and expression of this type of learning may involve the hippocampus. The fact that the two types of learning can occur at different times suggests that the hippocampus might be involved in recalling the spatial information, reorganizing, and re-storing it so that it is available for recall again during the test trial. To accomplish this two-way communication with the cortex is required, as has been suggested by at least one theory of hippocampal function (Moscovitch & Nadel, 1998).

The idea that the hippocampus has two-way communication with the cortex in producing behavior that results in ambiguous cue discriminations leads to the further suggestion that this kind of subcortical–cortical communication may be important for the function of all three systems. Each has afferent pathways that reach the cortex and are known to influence its function (e.g., Amaral, 1987; Groenewegen, Wright, & Uylings, 1997; Heimer & Wilson, 1975; Krettek & Price, 1977; Swanson, 1981; Turner & Zimmer, 1984; Wise, Murray, & Gerfen, 1996). To the extent that a influence from one system has lasting effects on a cortical representation of some learning situation, the nature of the information about that situation that flows from the cortex to all three subcortical systems may be altered when it is recalled. Evidence for this kind of indirect functional interaction among the systems is lacking at present.

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