# Preserved and Impaired Information Processing Systems in Human Bitemporal Amnesiacs and their Infrahuman Analogues: Role of Hippocampectomy

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An information processing model is proposed to account for the dissociation of amnesia and spared learning capacity in hippocampectomized organisms, including human bitemporal amnesiacs and their animal analogues. According to the model, the hippocampus is critically involved in an integrative cognitive process termed chunking, which mediates propositional learning, complex conditioning, and cognitive mapping. Hippocampectomy selectively impairs the chunking process, leaving intact pre-operatively consolidated information, and also hierarchical perceptual and motor systems. The proposed models of these latter systems account for hippocampectomized amnesiacs' spared capacity for associative learning and skill acquisition.

In 1954, Scoville reported the results of a surgical procedure he had developed to treat the intractable epilepsy of his patient, H.M. The operation involved the bilateral removal of epileptogenic tissues, including the hippocampus, amygdala, and hippocampal gyrus. The totally unexpected behavioral result of the surgery was a severe and generalized anterograde amnesia. In addition, the patient suffered from a partial retrograde amnesia. An extensive analysis of H.M.'s syndrome, carried out by Milner and her colleagues (Corkin, 1968; Milner, 1962; Milner, Corkin and Teuber, 1968; Scoville and Milner, 1957), confirmed what seemed apparent from casual observation: H.M.'s amnesia was extensive and extremely debilitating. Most obvious was his inability to recall the events of daily life minutes or even seconds after they occurred. Formal tests also revealed deficits in delayed matching-to-sample, visual and tactile maze tasks, tests of verbal learning and recall and various other tasks (e.g., Milner et al., 1968). However, a less obvious fact was also revealed by these tests: H.M. demonstrated some residual capacity for learning. One of the first

demonstrations of his spared mnemonic function was obtained by Milner in 1960, when she found that H.M. acquired skill in the mirror-tracing task at a normal rate (Milner, 1970). Since this time, H.M.'s ability to acquire motor skills has become well known. However, his spared learning capacity is not limited to motor skills: for example, Milner (1970) also found that H.M. is capable of the long-term retention of certain perceptual information. More recently, a dramatic example of H.M.'s spared learning capacity has been provided in the demonstration of his ability to solve the Tower of Hanoi puzzle at a normal rat (Cohen, 1984).

H.M. has been more extensively studied than any other human bitemporal amnesiac. However, since his case was first reported, a number of other patients having amnesia of confirmed or suspected bitemporal etiology have been described. Investigations of these cases have revealed a pattern of deficits and spared learning similar to that described for H.M. (e.g., Muramoto, Kuru, Sugishita and Toyokura, 1979; Penfield and Mathieson, 1974; Squire and Zola-Morgan, 1983). Furthermore, a similar dissociation of amnesia and spared learning capacity obtains in infrahuman analogues of human bitemporal amnesiacs; that is, the capacity to acquire and retain information in some tasks is spared, while in other tasks the animals are amnesic.

In this paper, a cognitive model is developed to account for the dissociation of amnesia and spared learning capacity that obtains in hippocampectomized organisms, including human bitemporal amnesiacs and their infrahuman analogues. The model is based, in part, upon Wickelgren's (1979) hypothesis that hippocampectomy selectively impairs an integrative cognitive process termed chunking. The chunking process stores previously discrete bits of information as an integral unit termed a chunk node. A cognitive system of organized chunk nodes is here termed a chunking system. According to the proposed model, the amnesia that obtains following hippocampectomy is primarily a deficit in storing and consolidating information within the chunking systems.

The model further proposes that amnesiacs' spared learning capacity, including their ability to acquire complex and flexible motor programs, is mediated by hierarchical perceptual and motor systems that remain intact following hippocampectomy and bitemporal lobectomy. Interconnections between the upper levels of these systems mediate the amnesiacs' capacity for simple associative learning.

The model proposed here begins with the premise that the critical lesion in bitemporal amnesia is hippocampectomy. This hypothesis, originally advanced by Scoville and Milner (1957), has recently been challenged (Horel, 1978; Mishkin, 1978). In the following section, data bearing on this issue are briefly reviewed.

## The Etiology of Bitemporal Amnesia

Scoville and Milner (1957) found that medial temporal surgery caused amnesia only when the resection included the hippocampus. Resection of the temporal lobe anterior to the hippocampus, including the amygdala, did not result in amnesic deficits. From these data, the authors concluded that hippocampal damage is critical to the production of the amnesic syndrome. This conclusion received further support from studies of patients who had undergone unilateral temporal ablation. Such patients generally suffer from a relatively mild amnesia that is specific to certain types of information (Milner, 1970). Milner and her colleagues have found that the severity of the anterograde amnesia following unilateral temporal lobectomy is correlated with the extent of hippocampal damage (Milner, 1970).

Infrequently, unilateral hippocampal resection has resulted in severe amnesia, similar to that of H.M. Penfield performed an autopsy on one such patient (Penfield and Mathieson, 1974) and found that the non-resected hippocampus was necrotic. This and other findings led Penfield to confirm an already generally accepted hypothesis: that bilateral hippocampal damage is critical to the production of the amnesic syndrome.

Recently, this hypothesis has been re-evaluated by Horel (1978) and by Mishkin (1978). In his thorough review, Horel notes that severe damage of the temporal stem generally accompanies hippocampal ablation. On the basis of this and other evidence, he proposes that damage to the temporal stem, and not the hippocampus, is the critical lesion in bitemporal amnesia. However, a recent experimental test failed to confirm Horel's hypothesis (Zola-Morgan, Squire and Mishkin, 1982). In this study, monkeys with conjoint hippocampal and amygdalar lesions and monkeys with temporal stem lesions were compared in the post-operative acquisition of a delayed nonmatching-to-sample task. Only monkeys with conjoint hippocampal and amygdalar lesions were impaired in task acquisition; monkeys with temporal stem lesions were unimpaired relative to controls. Similarly, in another study, hippocampally lesioned monkeys were impaired in the concurrent performance of post-operatively acquired visual and tactile discrimination tasks, even though the temporal stem in these subjects was entirely spared (Moss, Mahut and Zola-Morgan, 1981). These data suggest that damage to medial temporal structures other than the temporal stem is critical to the production of bitemporal amnesia.

A second influential alternative to the hypothesis that hippocampectomy is the critical lesion in amnesia was proposed by Mishkin (1978), who found that unilateral or bilateral amygdalar resection greatly exacerbated the impairment of hippocampectomized monkeys in the performance of a pre-operatively acquired nonmatching-to-sample task. He also noted that, in cases of human bitemporal amnesia, unilateral or bilateral amygdalectomy generally accompanies hippocampal damage. His hypothesis, then, is that the amygdala and

hippocampus are involved in separate, redundant, memory circuits.

Squire and Zola-Morgan (1983) have critically reviewed the data bearing on this proposal. In particular, they note that in joint hippocampal-amygdalar resections, generally only the anterior third of the hippocampus is ablated. However, in lesioning the hippocampus alone, a posterior approach is often used. In this case, the anterior one-third of the hippocampus is spared, and the posterior two-thirds ablated. The authors conclude that, because of procedural problems such as these, the extant evidence in support of Mishkin's hypothesis cannot be considered compelling.

A recently reported case of human bitemporal amnesia of vascular origin provides further evidence against Mishkin's hypothesis (Woods, Schoene and Kneisley, 1982). Severe amnesia developed in a patient following embolic stroke and persisted until her death nine months later. Post-mortem histology revealed a large lesion of the medial temporal-occipital region of the left hemisphere. The lesion in the right hemisphere was confined to the hippocampus and subiculum. Neither of these lesions involved the amygdala; bilaterally, this structure was intact.

The above reported cases notwithstanding, it would be naive to suggest that amygdalar damage does not contribute to the amnesic syndrome of H.M. and of other bitemporal amnesics. On the contrary, as stated above, in certain cases the degree of amygdalar damage seems to be related to the severity of the performance deficit (Mishkin, 1978; Mishkin, Spiegler, Saunders and Malamut, 1982). However, this finding does not obtain in all tests of anterograde amnesia; in some tasks used with non-human primates, both hippocampectomized animals and those which have conjoint lesions are severely impaired (Squire and Zola-Morgan, 1983). The data briefly reviewed here support the hypothesis that while amygdalectomy may contribute to certain manifestations of the amnesic syndrome, hippocampectomy is critical for the development of severe generalized amnesia. In this paper, I will concentrate on the amnesic effects of hippocampectomy, and will leave the consideration of the role of amygdalectomy (and of the interactive effects of conjoint lesions) to future endeavors.

In discussing amnesic deficits, data from the large literature concerned with the effects of hippocampectomy in infrahumans will be cited. On the other hand, it is reasonable to assume that functions spared following large lesions of the medial temporal regions are also spared following hippocampectomy. Therefore, the model presented in the following section accounts directly for amnesic deficits in hippocampectomized organisms, and spared functions in human bitemporal amnesics. Furthermore, the model provides a framework for the future discussion of the human bitemporal amnesic syndrome.

## Information Processing in Intact and Hippocampectomized Organisms

Considerable evidence from cognitive psychology (Konorski, 1967; Martindale, 1981; Nadel, 1981), neuropsychology (e.g., Mishkin, 1979), and developmental psychology (Nadel and Zola-Morgan, in press) suggests that multiple systems of information processing, each specialized for a different informational content, mediate mnemonic abilities of humans and infrahumans. These systems are conceived of as organized networks of interrelated bits of information. The storage site for each bit of information is termed a node. While the content of a node is being processed (e.g., retrieved), that node is referred to as activated. Connections conduct activation processes from one node to another related node. The activation of nodes and their connections has a strengthening effect, and these strengthening processes lower the nodes' thresholds for future activation.

The model proposed here distinguishes between two categories of systems: The first category consists of systems that are involved directly in organizing sensory receptor input (the perceptual systems) and effector organ output (the action system). The second category of systems, here termed chunking systems (Wickelgren, 1979), are organized structures of complex cognitive units (e.g. propositions, [Anderson, 1980], or compound stimulus information). These units, termed chunk nodes, represent integrated groups (or "chunks") of related perceptual and motor information. In addition, chunk nodes may be hierarchically organized, such that upper level chunk nodes represent the integrated content of two or more lower level chunk nodes. The model assumes that the chunking process mediates all cognitive learning in organisms having hippocampi.

These systems and their proposed functions can account for the dissociation of preserved and impaired learning processes in the hippocampectomized amnesiac. Hippocampectomy selectively impairs the chunking *process;* that is, hippocampectomized organisms are unable to form new chunk nodes to mediate new cognitive learning. Furthermore, this process of chunking is, in part, a consolidation process. Following hippocampectomy, only completely consolidated nodes are spared. These hypotheses account for the findings that the retrograde amnesia of hippocampectomized humans and infrahumans is partial and has a temporal gradient (e.g., Marslen-Wilson and Teuber, 1975; Squire, Cohen and Nadel, 1983).

The perceptual and action systems and their interconnections are spared following hippocampectomy. These systems mediate perceptual and motor learning (including recognition and skill learning). In addition, connections between the upper levels of these hierarchical systems form an associative system that exclusively mediates the association of contiguous perceptual and motor events.

## Perceptual Systems

Cognitive theorists have frequently assumed that perceptual systems are hierarchically organized, and this view is incorporated here. (See Konorski [1967] and Martindale [1981] for a more detailed treatment of this topic than can be pursued here.) A separate system mediates each type of stimulus information, including visual objects, auditory stimuli, morphemes, and printed words. Each of these proposed systems has three levels:

(1) Upper level nodes, here termed percept nodes, represent the objects of perception (Konorski, 1967).

(2) Intermediate level nodes code the perceived components of objects; for example, a door handle is a perceived component of a door.

(3) Lower level nodes code the elemental features of an object (Hubel and Wiesel, 1965). These features may or may not be accessible to consciousness; that is, even though one may be unaware of the component waveforms of some non-primary color, these waveforms are analyzed by the perceptual system as features.

Each percept node is interconnected, via ascending and descending connections, with several intermediate level nodes (coding its components); these, in turn, are interconnected with a series of lower level nodes coding its features. Thus each percept node governs a hierarchy—the percept hierarchy—of interconnected lower and intermediate level nodes.

The assumption that perceptual systems are spared following hippocampectomy accounts for perceptual learning in amnesics (e.g., Iversen, 1977). Consider, for example, the performance of H.M. on the Gollin's Incomplete Pictures task, in which subjects are presented with a series of cards bearing progressively more complete line drawings of some common object. Subsequently, their ability to recognize the incomplete drawings is tested. Although H.M. did not remember his involvement in the task, his error score was reduced in testing one hour after initial exposure to the series and also 4 months later (Milner et al., 1968). Unimpaired subjects presumably utilize higher order cognitive systems to code additional information, perhaps including semantic information regarding the list of items included on the task (Milner et al., 1968, p. 231). Such information would clearly aid retrieval and would account for the superior performance of normals.

Recently, H.M.'s ability to identify repeated and non-repeated words also has been investigated (Nissen, Cohen and Corkin, 1981). H.M.'s performance on this task was evidence of his spared recognition ability: after intervals of 1 hour or 1 day, he identified more repeated than non-repeated words. In addition, his skill in identifying all words, including non-repeated words, improved with practice.

Recently developed theoretical accounts propose that perceptual recognition (Mishkin, 1982) and perceptual skill acquisition (Cohen, 1984) are functions of

the perceptual systems themselves. Thus, these spared abilities can be accounted for by assuming that connections among nodes in the activated percept hierarchies are strengthened by use. This strengthening process lowers the threshold of affected nodes for re-activation. For example, repeated words activate an entire percept hierarchy that has been previously strengthened. On the other hand, improvement in the identification of non-repeated words is mediated by the strengthening of middle and lower level nodes (for letters and their features) that are shared by many words.

Perceptual learning also is spared in infrahumans, as evidenced by findings that hippectomized monkeys and rats are generally unimpaired in the acquisition of simultaneous discrimination tasks (Gray, 1982: Isaacson, 1974; O'Keefe and Nadel, 1978; Squire and Zola-Morgan, 1983).

Particularly compelling evidence of spared perceptual learning following hippocampectomy is provided by studies of monkeys' performance in non-matching-to-sample paradigms with trial-unique stimuli. This task requires the subject to choose the novel object of a pair following a brief period of familiarization with the other object of that pair. (See Mishkin and Delacour, 1975, for a more complete description of this task.) Unoperated monkeys are highly accurate in their performance of this task, generally choosing the correct object on well over 90% of the trials. Hippocampectomy has little (Mishkin, 1978) or no effect (Delacour, 1977) upon the performance of pre-operatively trained monkeys. Post-operatively trained monkeys exhibit a more marked deficit (Mahut, Zola-Morgan and Moss, 1982): they are impaired in attaining criterion, and at the longest intervals investigated (approximately one and two minute intervals) they are impaired relative to normals in asymptotic performance.

Mishkin's (1978; Mishkin and Delacour, 1975) analysis of the performance of normal monkeys in this task suggests an interpretation of the behavior of hippocampectomized monkeys that is consistent with the proposed model. He has noted that, when presented with a novel and a familiar object in a delayed nonmatching-to-sample procedure, normal monkeys exhibit "a natural tendency to choose the novel object" (Mishkin, 1978). For example, Mishkin and Delacour (1975) observed that unoperated animals achieved a level of 80% correct in each of their first two 20-trial sessions, and that their performance level was further improved to a 90% criterion within an average of 4.5 sessions. This rapid acquisition can be attributed to two factors: the spontaneous tendency to choose the novel object, and acquisition of the "correct principle" (Mishkin and Delacour, 1975, pp. 328–329). According to the model of the chunking system—discussed in detail below, the "correct principle" is a rule or propositional statement that represents the task contingencies and is stored within the chunking system.

Thus the model accounts for the findings, reported above, that post-operatively trained hippocampectomized monkeys are impaired, but only moderately so, in acquisition of the nonmatching-to-sample task: Hippocampectomy

does not affect their inherent preference for novelty, or their ability to recognize a similar stimulus, and these spared processes mediate their ability to perform this task. However, although these subjects did acquire the task, they were impaired in acquisition relative to normals. This impairment is attributed to a failure to encode propositional information that normals utilize to achieve highly accurate performance. Furthermore, by this account, the capacity of pre-operatively trained monkeys to achieve highly accurate levels of performance—similar to those of normals (Delacour, 1977; Mishkin, 1978)—is attributable to their retention of pre-operatively acquired propositional information regarding the task contingency.

In this section, the hypothesis that a complex perceptual system remains functional following hippocampectomy is applied to account for perceptual skill and recognition learning in hippocampectomized amnesiacs. A similar hypothesis accounts for spared motor learning. More interestingly, the assumption that the proposed systems are interconnected accounts for various types of perceptual control over motor behaviors, including both skills and elicited responses. Discussions of these topics follow.

### The Action System

The action system is a hierarchically structured network of nodes storing information regarding the execution of motor behaviors. Any organized, goal-directed, motor behavior is here termed an action (e.g., Newell, 1978); its neural substrate within the action system is termed a motor program. The types of actions mediated by these programs range from the "simple" operant bar-press, to the complex set of behaviors involved in the skill of playing tennis.

Many motor programs mediate actions that are highly adaptable (MacKay, 1982); that is, they can be modified during their execution by perceptual and propositional input. Three assumptions regarding the structure of a motor program hierarchy can account for this adaptability: (a) Most actions consist of a sequence of separable component behaviors; (b) each component behavior is stored as an independent sub-program within the motor program; and (c) these sub-programs can be either automatically "run-off" in sequence, or individually accessed (Newell, 1978).

The proposed action system has three levels. Nodes within the respective levels control motor programs, their sub-programs, and specific muscle movements:

1. Upper level nodes, here termed action nodes, represent integrated information regarding the execution of actions (e.g., opening a door). Via neural connections, each action node controls a hierarchy of middle and lower-level nodes. This hierarchy of interconnected nodes is the motor program.

2. Middle level nodes, termed sub-program nodes, represent the movements that are components of an action (e.g., "grasping a doorknob" is a component

of the "opening a door" action). Sub-program nodes may be arranged in sequence or in parallel (cf. Hayes and Marteniuk, 1976). For example, the nodes for grasping, turning, and pulling a doorknob are arranged in sequence. However, because the action of pushing a door is an alternative to pulling, the nodes for these behaviors are stored in parallel.

Sub-program nodes also receive input from sources external to the action system. Thus, a sub-program may be individually accessed; also, a sequence of sub-programs may be initiated at any point.

3. Each sub-program node controls a system of feature nodes; these, in turn, control the specific activity of individual motor units (e.g., muscle fiber contractions). The interconnections among feature nodes govern the patterns of muscle activity involved in the execution of each sub-program.

The model proposed here is consistent with the idea, more completely developed elsewhere (e.g., MacKay, 1982) that actions can be accounted for by assuming that the motor program hierarchy for any action includes a series of sub-programs, and that these sub-programs can be activated independently of the entire motor program hierarchy.

### Interaction of the Perceptual and Action Systems

The perceptual and action systems are interconnected at all levels. The model proposes that these systems and their interconnections mediate all new learning in amnesics.

### The Associative System

All associative learning exhibited by hippocampectomized organisms is mediated by the strengthening of previously non-functional connections between percept and action nodes. A few straightforward hypotheses regarding these connections can account for the large extant literature concerned with the performance of hippocampectomized organisms in operant and classical conditioning procedures:

1. The principle of contiguity governs the formation of associations between percept and action nodes. That is, when a response (controlled by an action node and its motor program) is followed by reinforcement, an association is formed between that response and its antecedent stimuli (represented by percent nodes). (Possible neural mechanisms for such effects have been discussed in detail elsewhere, e.g., Kandel, 1976; R.Y. Moore, 1976; Rutledge, 1976). The occurrence of reinforcement activates neural arousal systems (Rolls, 1975) that greatly enhance the strengthening effects of stimulus-response pairing.

Evidence in support of the hypothesis that the contiguity principle accounts for associative learning in hippocampectomized organisms, but not in organisms having hippocampi, is discussed later in this paper.

2. The percept-action node association is not protected from interference. For example, many percept nodes, (each representing distinct stimuli) may become associated with one action node. In this case, any or all of the stimuli represented by these percept nodes may elicit the reinforced response. The converse process may also occur; a single percept node may become associated with several action nodes.

3. Each reinforced stimulus-response pairing strengthens the association, to some maximum level.

4. However, the strength of the percept-action node association depends not only upon the proportion of reinforced trials, but also upon stimulus variables such as perceived salience. Thus, if two percept nodes compete to form associations with the same action node, the percept node coding the most salient stimulus will, other things being equal, form the strongest association with that action node.

5. Responses emitted in the absence of reinforcement inhibit the re-activation of the percept-action node association. Thus the behavior of the hippocampectomized organism during extinction depends upon the cumulative effects of these inhibitory processes and the strengthening processes that act during acquisition. However, the hippocampectomized organism forms no new associations during extinction training. Evidence in support of this hypothesis is discussed elsewhere in this paper.

6. The inhibiting effects of a non-reinforced response are small compared with the strengthening effects of a reinforced response.

*Acquisition.* The associative system mediates unimpaired acquisition of simple stimulus-response contiguity relations. Its operation is most evident in experiments designed to evaluate the effects of hippocampectomy upon performance of simple classical and operant conditioning procedures. For example, hippocampectomized infrahumans generally acquire operant bar-press (e.g., Schmaltz and Isaacson, 1967) and straight-alley tasks (e.g., Jarrard, Isaacson, and Wickelgren, 1964) at normal or above-normal rates (although speed of running measures are found to be decreased on straight alley tasks; e.g., Bloom and McFarlain, 1971). Furthermore, such subjects are capable of acquiring several non-interfering contiguity relations simultaneously. For example, in blocking procedures, hippocampectomized organisms form conditioned responses to both elements of the CS (Rickert, Bennett, Lane and French, 1978; Solomon, 1977).

Behavior mediated by the associative system has an automatic character: that is, responses are elicited by environmental or conditioned stimuli with which they have previously been paired. (The term "elicited" is used here to emphasize the hypothesis that the hippocampectomized organism is highly susceptible to stimulus control, and not to imply that the associative system mediates only respondent, to the exclusion of operant, conditioning.) According to the proposed model, this stimulus control is mediated by percept-action

node associations; behavior that is mediated by a percept-action node association is controlled by whatever stimulus the percept node represents. This control can be so effective that the hippocampectomized organism fails to be distracted by the presentation of a novel stimulus during ongoing task performance (Gray, 1982). Such indistractibility is not due to any general impairment of perceptual processes; that is, hippocampectomized organisms have no general deficit in their ability to detect (e.g., Gray and McNaughton, 1983, p. 148; O'Keefe and Nadel, 1978, p. 355), orient to (e.g., Crowne and Riddell, 1969), or explore (e.g., Capobianco, MacDougall and Foster, 1977; Kimble, 1976; but see O'Keefe and Nadel, 1978, p. 240-264) novel stimuli. Rather, their indistractability may be attributed to the inflexible control of their behavior by stimuli that have previously been paired with reinforcement. Experiments providing additional support for this hypothesis (e.g., Devenport and Holloway, 1980; Winocur, 1982) are discussed later in this paper.

Hippocampectomized organisms are impaired in the acquistion of contiguity relations only when the underlying associations are in mutual conflict. For example, during discrimination reversal training (e.g., Mahut, Moss and Zola-Morgan, 1981), hippocampectomized organisms must learn a new contiguity relation (between the previous CS- and the reinforced response); however, in this case, the prepotent association formed during the initial task may interfere with acquisition of the reversal task. Another example involves the acquisition of two conflicting associations in the same stimulus environment. Such a situation may occur during the initial training trials of a passive avoidance task following training on an approach task in the same apparatus. Interference effects such as those mentioned here are an important component of the amnesic deficit, and, in a subsequent section of this paper, are applied to account for the behavior of hippocampectomized subjects in reversal, passive avoidance, and other tasks.

*Extinction.* It follows from the hypotheses stated above that the behavior of hippocampectomized organisms is a function of the proportion of reinforced responses performed during training, but that they do not acquire information regarding the *pattern* of reinforced trials. For example, recent findings suggest that hippocampectomy abolishes the partial reinforcement extinction effect (Rawlins, Feldon and Gray, 1980; see Gray and McNaughton, 1983 for an analysis of conditions that reinstate this effect).

Following training in a series of successive acquisition and extinction sessions, intact organisms demonstrate progressively more rapid extinction in successive extinction sessions. In contrast, hippocampectomized organisms are increasingly resistant to extinction in successive sessions (Schmaltz and Theios, 1972). These findings are further evidence that hippocampectomized organisms do not acquire information regarding the pattern of reinforcement, as do normals; but that their behavior is a function of the proportion of reinforced to total responses.

Following training on a schedule of continuous reinforcement, resistance to extinction in hippocampectomized organisms is dependent upon the length of the inter-trial interval (ITI) that is used during extinction (Jarrard and Isaacson, 1965). (Extinction in intact subjects is relatively insensitive to length of the ITI.) At short ITIs, hippocampectomy has no effect upon resistance to extinction. However, resistance to extinction is increased if a relatively long interval separates extinction trials. This finding is consistent with the proposed model if it is assumed that inhibition "builds up" during massed extinction trials (cf. O'Keefe and Nadel, 1978, pp. 96–98).

Studies of spared learning in hippocampectomized infrahumans have been concerned primarily with the all-or-none occurrence of the reinforced response; there has been little analysis of the motor skills required to execute these responses. On the other hand, the spared motor learning of human amnesiacs has received considerable investigative and theoretical attention (e.g., Corkin, 1968; Milner, 1970). According to the model proposed here, the all-or-none performance of any learned motor behavior is mediated by an action program. Therefore, if one is interested in a fine-grained analysis of motor skill learning, one must consider the entire hierarchical program for that skill. The components that lend adaptability to a program are its sub-programs, coded by middle level nodes.

*Connections Mediating the Flexible Use of Motor Sub-Programs*

In hippocampectomized organisms, action programs for complex skills (as for instrumental behaviors) are elicited via percept-action node connections. However, the fact that a stimulus may reliably activate a particular motor program does not imply an unvarying *pattern* of activation for that program. Rather, the pattern of activation and therefore the exact component movements of the response may vary among trials. This fact has led some to question the notion of a motor program (e.g., Schmidt, 1975). However, as discussed above, a hierarchically structured motor program is capable of storing alternate sub-programs for any component behavior. These sub-programs can be individually accessed by sources external to the motor program, including percept nodes and propositional chunk nodes. Connections between the latter type of node and the sub-program node mediate the control of sub-programs by propositions (rules) in normals. Hippocampectomized amnesiacs, according to the proposed model, are incapable of forming new chunk nodes to store rules. Instead, connections between sub-program nodes and percept nodes are formed during acquisition, and these connections mediate the flexible use of motor sub-programs by amnesiacs.

The model proposed here accounts for the recent finding that H.M. is capable of solving the Tower of Hanoi puzzle (Cohen, 1984). This puzzle consists of five donut-shaped blocks of graduated sizes arranged in a tower on one of

three pegs. Subjects are required to move the tower, one block at a time. In addition, they are restricted from ever placing a larger block on top of a smaller one. A minimum of 31 moves is required for solution of this task. In normal subjects, the strategy that reliably produces this optimal solution is the goal-recursion strategy (Cohen, 1981; Simon, 1975). Subjects using this strategy learn the goal ("Move the 5-block tower to the goal peg.") and a set of recursive sub-goals (Cohen, 1981; Simon, 1975). Acquisition of the recursive strategy involves conceptualization of the task as a series of progressively smaller Tower of Hanoi problems.

H.M. acquired the Tower of Hanoi task at a normal rate. However, his behavior was markedly dissimilar to that of normals in one regard: he demonstrated poor insight into what he was learning (Cohen, 1984). Even during the eighth session, "despite near perfect performance, his commentary during each trial always sounded as if he were solving the puzzle for the first time" (Cohen and Corkin, 1981, p. 235). Furthermore, after he had acquired the task, and while engaged in the process of solving it, he denied that a solution was possible (N. J. Cohen, personal communication, August, 1983). Normals, on the other hand, do provide verbal evidence of insight into their learning of goals and sub-goals (e.g., Anzai and Simon, 1979; Cohen, 1981; Cohen, 1984). This difference between H.M. and normals is probably not due to differences in semantic ability (Milner et al., 1968, p. 216). Rather, it seems that H.M., unlike normals, failed to store goals or rules in memory. According to the model proposed here, he solved the puzzle by acquiring a motor program, and that program itself and its sub-programs are perceptually driven. That is, the 2-block, 3-block, and 4-block towers (as well as the 5-block tower) are each stored as percepts, and the actions of moving these towers are represented by the action and sub-program nodes.

*Connections Mediating the Effects of Perceptual Feedback Upon Muscular Movements*

The execution of certain skills requires continuous perceptually controlled fine-tuning of muscular movements (e.g., Kornhubber, 1974). An example of such a task is the mirror-tracing task involving the tracing of a reversed-image star. This task was acquired by H.M. at a normal rate (Milner, 1970). According to the model proposed here, connections between the perceptual (e.g., somatosensory) and feature nodes of the action system mediate the continuous perceptually controlled fine-tuning of muscular movements required for performance of this task. Practice strengthens these connections, improving speed and accuracy of performance. Thus, highly skilled performance on this and similar tasks is mediated not only by strengthened connections within the motor program, but also by strengthened connections between the perceptual systems and the relevant feature nodes of the action system.

Investigators agree that memory for fine-tuned perceptual motor skills such as that evidenced in the above cited mirror-tracing task is intact in amnesiacs. However, the issue of classifying the spared capacity of hippocampectomized amnesiacs for the acquistion of more complex skills (e.g., the Tower of Hanoi puzzle) and for associative learning is more controversial. In this discussion, I have argued that all spared learning capacity in amnesiacs is mediated by perceptual and motor processes, and have proposed a model that accounts for the behavioral manifestations of these processes.

In organisms having hippocampi, the utilization of a cognitive process termed chunking complements the percept and action systems during the acquisition of skills (or any other type of perceptual or motor learning). This assumption accounts for the fact that normals, but not hippocampectomized organisms, acquire goals and rules to mediate their performance of skills. Furthermore, the chunking process supersedes percept-action node interactions in all cognitive learning; that is, although a percept-action node association may adequately mediate acquisition of certain experimental tasks, normals always form one or more chunk nodes to mediate acquisition, and never rely upon a percept-action node association. This assumption is supported by abundant evidence that, in associative learning tasks, normal organisms always learn more than what is explicitly reinforced. They learn, for example, contingency relations (e.g., Devenport and Holloway, 1980) when contiguity relations would be effective, and cognitive maps when routes (stimulus-response chains) would be effective (O'Keefe and Nadel, 1978). The proposed model of the chunking system is developed in the following section.

## The Chunking System

Chunking is the process of establishing a neural storage site (the chunk node) for the purpose of representing the integrated informational content of two or more other sites (the constituent nodes). Chunk nodes and their interconnections comprise the higher-order cognitive systems. Constituents of chunk nodes may be percept nodes, action nodes, other chunk nodes, or some combination of these.

The chunk node functions as a unit; therefore, if one of its constituents is activated, the entire chunk is activated. Furthermore, chunk nodes are stored separately from each other; that is, they are protected from associative interference (Wickelgren, 1979). This protection is enhanced during the consolidation process.

### The Formation and Consolidation of Chunk Nodes

The proposed model assumes that abundant weak, potentially functional, connections join the action and percept nodes with potential chunk node sites.

When a percept and an action node are activated in contiguity, the activation spreads from these nodes into the higher order cognitive systems via ascending connections. The activation follows two pathways: a direct pathway, and an indirect one that synapses in the hippocampus. These pathways and the structures they connect are topographically organized. Therefore, the activation that spreads along both pathways converges on a single group of local circuit neurons; this group of cells is the hypothetical substrate of the chunk node. The hippocampus participates in the formation and consolidation of chunk nodes by strengthening the node itself and its connections with constituent nodes. When the consolidation process is complete, the hippocampal inputs to the chunk node are suppressed (Wickelgren, 1979).

*Role of the hippocampus in chunking.* The consolidation process takes time, and requires continuous or repeated activation. However, casual observation, as well as experimental evidence, attests to the fact that information often is stored following a brief experience and is retained indefinitely. Early attempts to find persistent synaptic changes in the mammalian CNS that might serve as mechanisms for such rapidly formed and long-lasting memories were unsuccessful. In fact, these experiments seemed to demonstrate that synaptic plasticity occurred only with parameters of stimulation that far exceeded those occurring *in vivo* (Eccles, 1979). More recently, however, investigators have demonstrated that a relatively mild tetanic stimulation of certain tissues produces a persistent potentiation of post-synaptically recorded evoked potentials. This effect is termed long-term potentiation (LTP).

LTP has a rapid onset, often occurring after application of a single tetanic stimulus of mild intensity. The effect also is persistent, and may last for days (Bliss and Gardner-Medwin, 1973; Bliss and Lomo, 1973), weeks (Barnes, 1979; Racine, Milgram and Hafner, 1983), or even months (Douglas and Goddard, 1975).

Although LTP has been demonstrated in several limbic tissues, the threshold for producing LTP is significantly lower in the hippocampus and in afferent and efferent pathways that are monosynaptically removed from the hippocampus (Racine et al., 1983). Furthermore, hippocampal sites tend to produce the most reliable, strongest, and most persistent LTP effects. These findings are consistent with the hypothesis that hippocampal processing is critical to information storage.

The model proposes that the specific function of hippocampal LTP involves consolidation of the chunk node. LTP potentiates the input of the indirect pathway to the chunk node, thereby augmenting the consolidating effects of constituent node stimulation. Furthermore, potentiated hippocampal-chunk node connections carry "non-specific" hippocampal electroencephalographic (e.g., theta) activity to the chunk node, thus greatly increasing the temporal parameters of chunk node stimulation. One consequence of this continued activation of the chunk node's local circuit neurons is that they are maintained

in a depolarized state; that is, their threshold for activation by direct connections is consistently lowered.

According to the model, both of these hippocampal processes—the augmented amplitude and frequency of activation—are required for the consolidation of the chunk node. Thus the hippocampus participates in the formation or storage of new chunk nodes and also their consolidation.

*The formation of descending connections.* Connections between a chunk node and its constituents are reciprocal. If the chunk node is activated, it subsequently activates its constituent nodes via descending connections. The strengthening of these connections is part of the consolidation process.

*The suppression of hippocampal connections.* The gradual strengthening of intrachunk synapses results in the gradual suppression of hippocampal connections with the chunk node (Mark, 1974; Wickelgren, 1979). Such a process would take days or weeks to complete. The consequence of the proposed lengthy process of suppression is to gradually increase the chunk node's resistance to associative interference. When hippocampal input is maximally suppressed, the chunk node can no longer subsume new constituent nodes, and therefore is maximally resistant to associative interference. However, the consolidated chunk node may become a constituent of another, higher-level, chunk node.

*Amnesia as a chunking deficit.* Thus, according to the model developed here, hippocampectomy interrupts the process of consolidation for recently formed chunk nodes, but has no effect upon completely consolidated nodes. Moreover, hippocampectomy precludes the formation and consolidation of new chunk nodes. In order to discuss the implications of these hypotheses for behavior, it is necessary to consider the types of chunk nodes that are formed in normal organisms, and the information they store.

## Types of Chunk Nodes

Two types of chunk nodes can account for the performance, in most learning tasks, of organisms having hippocampi: proposition nodes and stimulus complex nodes.

### Proposition Nodes

Of the possible types of propositions that may be stored in the chunking system, the conditional is of particular interest because it codes the contingency relations that control behavior in most learning tasks. The contingency relations that are extant in these tasks can be represented as propositions that code the relationship $S_1-R_1 \rightarrow K_1$; that is, in the presence of a particular stimulus ($S_1$), a certain response ($R_1$) produces consequence $K_1$. If $S_1$ and $K_1$ are perceptual events, they are coded by percept nodes and their corresponding hierarchies. $R_1$

is coded by an action node and its hierarchy. The three nodes are connected, via ascending and descending connections, with a propositional chunk node. When the chunk node is activated by one of the constitutent nodes (e.g., $S_1$), the activation is conducted via descending connections to nodes coding $R_1$ and $K_1$, thereby activating its constituent percept and action program hierarchies. This descending activation process is the substrate of recall, and accounts for the ability of intact subjects to anticipate the consequences of a response (i.e., to code contingency relations). The actual emission of a response depends upon additional processes, including motivation, that are beyond the scope of this paper.

   *The contingency principle versus the contiguity principle.* The proposed model predicts that intact organisms code contingency relations, while hippocampec-tomized organisms (utilizing the associative system) code contiguity relations. However, in many tasks, the contingent event (e.g., food delivery) is also spatially and temporally contiguous with the instrumental response and its antecedent stimuli. Such tasks are insensitive to the different operating princi-ples of the chunking and the associative systems. However, an elegant series of studies by Devenport (Devenport, 1979, 1980; Devenport and Holloway, 1980) demonstrates the differential operation of the contingency and contiguity principles in hippocampectomized and control rats. Devenport (1980) investi-gated the bar-pressing behavior of these two groups during the delivery of noncontingent reinforcement. Although control rats emitted only 4 or 5 responses per 90 minute session, hippocampectomized rats responded hundreds of times. Furthermore, Devenport and Holloway (1980) demonstrated that the effects of noncontingent pellet delivery are better accounted for by the Skin-nerian supersitition hypothesis (Skinner, 1948) than by Staddon's theory of schedule-induced behavior (Staddon, 1977; Staddon and Simmelhag, 1971). These findings provide compelling support for the proposed model.

   *Compound conditional propositions.* Related conditional propositions are organized hierarchically. Separate chunk nodes simultaneously maintain two or more distinct conditional propositions; these constitute one level of the hier-archy. A compound conditional stored at a higher level codes the relationship among these constituent nodes. This proposal accounts for the ability of organisms to simultaneously maintain separate but related conditionals, as is evident in their ability to acquire learning sets and conditional discriminations.

   *Propositional chunk nodes storing non-conditional information.* Propositional chunk nodes do not store conditional information exclusively; they also store other types of declarative propositions (cf., Squire, Cohen and Nadel, 1983). For example, there is evidence that humans store a series of declarative propositions representing goals and sub-goals to mediate performance of the Tower of Hanoi task (e.g., Anderson 1980; Anzai and Simon, 1979). The storage of conditional information, and therefore of contingency information, is emphasized here because this particular type of proposition can be applied to account for the

behavior of various species in a large proportion of experimental learning tasks. This topic is pursued further in the analytical literature review that follows the proposal of the second type of chunk node.

*Stimulus Complex Nodes*

The stimulus complex node is a chunk node that is interconnected with two or more percept nodes—its constituents—via ascending and descending connections. If the chunk node is activated by one constituent, it will, in turn, activate its remaining constituents via descending connections. By this process, a group of related perceptual events may be recalled as an integral unit.

Two major functions of stimulus complex nodes are considered here: their proposed roles in mediating classical conditioning and cognitive mapping.

*Classical conditioning.* Intact organisms do not form associations among all contiguous stimuli. In numerous experimental procedures, organisms respond to paired or grouped stimuli as integral units. For example, in the blocking procedure (Kamin, 1969), training with a $CS_A$-US pair precludes the formation of a $CS_B$-US association. According to the proposed model, the blocking effect occurs because, before $CS_B$ is introduced, the $CS_A$-US pair has been stored within a stimulus complex chunk node. The informational contents of this node are protected from associative interference, thus preventing the formation of a direct $CS_B$-US association. The model also accounts for Kamin's finding that the blocking effect is not obtained if the $CS_B$ signals a new US. In this case the chunking process integrates the two unique percept nodes for the $CS_B$ and the new US, forming a second stimulus complex node. Thus, according to the present model, classical conditioning is not a simple associative process; it is an integrative (chunking) process.

An elegant series of electrophysiological and ablation experiments conducted by Thompson and his colleagues (e.g., Berger and Orr, 1983; R.F. Thompson et al., 1980) have provided considerable insight into the role of the hippocampus in classical conditioning. The results of these experiments provide support for the proposed model.

In the electrophysiological experiments, hippocampal single unit activity was recorded during classical conditioning of the rabbit's nictitating membrane reflex. This activity precedes and reliably predicts the development of the CR across trials. Within trials, the amplitude and the time course of the CR are modelled by the unit activity; that is, the pattern of activity correlates closely with the pattern of the CR. (In some cases, the correlation coefficient is as high as .90.) Yet, such hippocampal activity is not critical to the production of the CR (e.g., Berger and Orr, 1983).

Furthermore, when paired and unpaired trials are alternated (Hoehler and Thompson, 1979) the potentiated hippocampal responses reflect a learning of the pattern of reinforcement. These findings, and numerous controls not

reviewed here, have established that the hippocampal neural response occurs only as the consequence of pairing the CS and US events. This plasticity may reflect the operation of the chunking process.

This interpretation receives support from a recent investigation of the effects of hippocampectomy upon acquisition of a conditioning task and its reversal by Berger and Orr (1983). These authors paired a 1 kHz tone with an airpuff and a 10 kHz tone with the absence of an airpuff. Hippocampectomized rabbits performed as well as normals in the original conditioning task, but were severely impaired when the contingencies were reversed.

The proposed model of the chunking system accounts for the behavior of the control subjects in this task by assuming that they formed stimulus complex nodes to separately represent the original $CS^+$–US and $CS^-$–no US pairs. Following reversal training, a new set of chunk nodes was formed to represent the reversed contingencies. The superseded and current chunk nodes are protected from associative interference, thus facilitating the reversal process (Wickelgren, 1979).

In the hippocampectomized organism, conditioning is represented by the formation of a percept-action node association between nodes for the CSs and CR. The association is strengthened by the occurrence of the US. The $CS^+$–CR association mediates unimpaired performance of the initial task. During reversal training, the initial $CS^-$ becomes associated with the same CR. Thus, as Berger and Orr (1983) report, the hippocampectomized rabbits' deficit during reversal training was due to their continued responding to the initial $CS^+$; they were unimpaired in learing to respond to the new positive CS.

Note that the hippocampal unit activity changes referred to above were recorded during a simple conditioning task (not a reversal task). Yet, following hippocampectomy, subjects are unimpaired in acquisition of such a task; rather, they are impaired only when the task is maximally sensitive to associative interference, as in the case of this reversal task.

The present model resolves this apparent discrepancy by proposing that control subjects utilize the chunking system during both initial and reversal training conditions. Hippocampectomized organisms are forced to rely upon an alternative system which is an effective substitute of the chunking system only during the initial simple associative task. Thus, according to this account, the control and hippocampectomized subjects do utilize different cognitive systems, but only the reversal task, and not the initial task, is sensitive to the differences between the systems.

*Spatial tasks.* Considerable evidence supports the position that the spatial abilities of intact organisms are mediated by a hypothetical construct termed a cognitive map—a nonegocentric representation of the spatial environment (e.g., Menzel, 1978; Nadel and Zola-Morgan, in press; O'Keefe and Nadel, 1978). This representation is very likely abstract and non-isomorphic (Uttal, 1978). Maps lend considerable flexibility to behavior; an organism relying on a map

can find a particular location from any starting point.

Cognitive maps include information regarding specific places and their relative locations. There is evidence that each place is defined by a unique set of cues (e.g., O'Keefe and Conway, 1978; O'Keefe and Nadel, 1978). However, no one cue is essential in identifying a place. Rather, the neural place representation can be activated by some proportion of the members of the set of cues (O'Keefe and Nadel, 1978, pp. 205–209). Furthermore, activation of the place representation will cause the organism to expect to find the remaining members of the set in their familiar locations. If a cue is missing, the organism will display species-characteristic novelty reactions (Nadel and Willner, 1980; Nadel, Willner and Kurz, 1984).

The concept of a stimulus complex node as a storage site of integrated perceptual information is similar to this idea of a place representation. Therefore, I suggest that stimulus complex nodes may code sets of cues that define places. For brevity, these nodes are referred to as place nodes.

Place nodes receive input from percept nodes representing individual environmental cues. These constituent nodes primarily code discrete visual and other sensory cues (e.g., Zoladek and Roberts, 1978) but may also code optical and kinesthetic/proprioceptive spatial information (e.g., Eriksson, 1974). A place node can be activated by a subset of constituent nodes; in turn, it partially activates its remaining constituents. This latter process is the substrate of expectancy (cf. Nadel et al., 1984). That is, the partially activated nodes provide the organism with information regarding what stimuli it can expect to find at a particular location.

A cognitive map is an organized network of place nodes and their spatial interrelations. This construct accounts for the ability of intact organisms to behave flexibly in spatial tasks. In contrast, hippocampectomized organisms utilize the associative system to mediate acquisition of such tasks. Therefore, hippocampectomized organisms should perform poorly in spatial tasks that cannot be mediated by one or more percept-action node associations.

In the next section, the performance of hippocampectomized organisms in tasks sensitive to the differences between the chunking and the associative systems is reviewed.

### The Amnesic Consequences of Hippocampectomy

The amnesic symptoms of hippocampectomized organisms are a simultaneous reflection of their inability to perform the chunking process and their consequent dependence upon an alternative associative system. These symptoms are evident only in tasks that are sensitive to the differences between the proposed systems. In this section, the model is applied to account for the behavior of hippocampectomized and control organisms in three categories of such tasks:

1. Instrumental learning tasks involving the acquisition of conflicting

contingency relations (e.g., reversal tasks).

2. Classical conditioning tasks involving the acquisition of information regarding the relative predictive value of conditioned stimuli.

3. Complex spatial tasks.

This review is limited to the effects of large hippocampal lesions; data obtained from subjects having small localized lesions are not discussed. For reasons detailed in the introduction to this paper, the effects of ablations extending to extrahippocampal structures are also left for future consideration. These limitations necessitate omission of much human data because (as also discussed previously) hippocampectomy in humans is generally accompanied by significant damage to other medial temporal structures. This discussion, then, is concerned with the amnesic effects of large hippocampal lesions in infrahumans.

### Consequences of the Hippocampectomized Organism's Inability to Form Propositional Chunk Nodes

The chunking system mediates the ability of organisms to acquire information regarding the consequences of their behavior. The advantages of this ability are best illustrated by considering the demands of instrumental tasks requiring the acquisition of two or more contingency relations. For example, in reversal tasks, two propositional chunk nodes are formed to represent the initial and reversal contingency relations. Each of these propositions is stored individually and is protected from associative interference. These propositional chunk nodes are interconnected in hierarchical fashion with a higher level chunk node coding a compound proposition that represents the initial and reversal contingencies and their temporal interrelationship (Wickelgren, 1979). Activation of one chunk node results in activation of the entire hierarchy; this activation is the substrate of information recall, and permits the organism to utilize information regarding the outcome of the previous trial or condition in choosing to emit a response. Mackintosh (1974, pp. 162–164) has reviewed compelling evidence that intact organisms do utilize such information. The model thus accounts for the ability of intact organisms to anticipate successive reversals (e.g., Riopelle, Alper, Strong and Ades, 1953). A similar account applies to the acquisition by intact animals of differential reinforcement of low rates (DRL) schedules following training on a continuous reinforcement schedule, of approach-avoidance tasks, of conditional discriminations, and, in fact, of any task or series of tasks involving the acquisition of separate but related contingencies. The following is a review of the effects of hippocampectomy on performance in such tasks.

*Reversal Tasks*

Two types of reversal tasks are considered here: position reversal tasks and stimulus discrimination reversal tasks. In the former task, organisms are trained to approach one side of a Y- or T-maze (rats) or one of two food wells (monkeys). When this initial task has been learned to criterion, the subjects are trained to approach the arm or the food well at the opposite side of the maze. Re-testing on the initial and reversal tasks may follow for several successive sessions. In stimulus discrimination reversal tasks, subjects initially learn to discriminate between an $S^+$ and $S^-$ with spatial cues counterbalanced across presentations. Upon acquisition of this discrimination, the $S^+$ and $S^-$ are reversed. Often the subjects are trained in several successive reversals.

Hippocampectomized rats (Greene, 1971; Samuels, 1972; R. Thompson, 1983; R. Thompson, Langer and Rich, 1964) and monkeys (Jones and Mishkin, 1972; Mahut, 1972) are impaired in performance of the position reversal task. However, experiments designed to assess the ability of hippocampectomized rats and monkeys to acquire discrimination reversal tasks have yielded equivocal results. Thus hippocampectomized monkeys are unimpaired in the acquisition and performance of object discrimination reversals (Jones and Mishkin, 1972; Mahut, 1971); but they are impaired in visual pattern discrimination reversals and in tactile discrimination reversals (Mahut, Moss and Zola-Morgan, 1981). Rats are also severely impaired in the acquisition of visual pattern reversals (Winocur nd Olds, 1978). Experiments designed to investigate the ability of hippocampectomized rats to acquire a brightness discrimination also have yielded equivocal results ranging from a severe deficit (Silveira and Kimble, 1968) to no deficit (R. Thompson, 1982a, 1982b). The reasons for the discrepant results obtained in these latter (brightness discrimination) studies are not clear. However, the general findings that hippocampectomy consistently produces severe impairments of position habit reversal performance, but produces more equivocal effects in stimulus discrimination reversal tasks, is accounted for by the proposed model.

According to this model, it is the relatively greater importance of spared perceptual processes in mediating the performance of stimulus reversal tasks, as compared to the position reversal tasks, that accounts for these differences. In the position reversal task, the correct and incorrect choices are not specifically cued, whereas in the stimulus reversal task, the discriminative stimuli designate the correct and incorrect choices. Furthermore, there is some evidence that hippocampectomized organisms are able to acquire the stimulus reversal task only if the $S^+$ and $S^-$ are highly discriminable. Thus, for example, Mahut et al. (1981) found that hippocampectomized monkeys were impaired when the 2-dimensional stimuli had only "subtle differences in pattern" (Mahut et al., 1981, p. 210). However, hippocampectomized monkeys are unimpaired when the discriminative stimuli are 3-dimensional objects that differ from each other

in several stimulus dimensions; for example, Mahut (1971) found that monkeys were unimpaired in such a task when a few paper clips versus a red plastic tomato were used as discriminative stimuli. Similarly, Winocur and Olds (1978) found that the hippocampectomized rat's deficit in visual pattern reversal tasks is reduced when contextual cues differed in the initial and reversal conditions. The effect of this manipulation may be attributed to the increased discriminability of these conditions.

The proposed structure of percept-action node associations accounts for the differential role of perceptual processes in mediating performance of the position reversal and stimulus reversal tasks. In the former task, the percept nodes coding chamber stimuli are not differentially associated with the two action nodes representing the conflicting alternative choices. In this case, percept node activation is conducted to the action node with which it is most strongly associated.

On the other hand, two distinct percept nodes represent the discriminative stimuli in the stimulus reversal task. Each of these nodes is connected with the same action node, which represents an approach or grasping response directed towards the eliciting stimulus. At any given moment, two variables determine the relative levels of activation of the percept-action node associations: (a) Associative strength: As a consequence of training variables, one of the percept nodes may be differentially associated with the action node; and (b) Perceptual processes: as a consequence of perceptual processes, including attention, one percept node may, at any given moment, be more strongly activated than another. To the extent that spared perceptual processes are substrates of performance on the stimulus reversal task, that performance should be unimpaired following hippocampectomy. It is reasonable to assume that, if easily discriminable stimuli are used, the utilization of perceptual processes in acquisition of the task is maximized (e.g., differential activation of the percept nodes as a consequence of attentional shifts would be maximized, Martindale, 1981). In this case, relative percept node activation as well as relative associative strength would be important factors in eliciting a particular choice.

The hypothesis that hippocampectomized organisms are most severely impaired when conflicting responses are elicited by the same stimulus (or the same stimulus environment) also accounts for findings obtained in approach-avoidance paradigms.

*Passive Avoidance*

Investigators consistently report that hippocampectomized subjects are impaired in acquiring a passive avoidance response following approach training in the same apparatus (e.g., Isaacson and Wickelgren, 1962; Kimble, 1963; Kimble, Kirkby and Stein, 1966; Riddell, 1966; Stein and Kirkby, 1967; Winocur

and Bindra, 1976). These findings are accounted for by the model of the associative system: acquisition of the appetitively motivated approach task is mediated by the formation of an association between nodes coding environmental stimuli and the approach response. During avoidance training, a new association is formed between the original percept nodes coding environmental stimuli and an action node coding an avoidance response. The hippocampectomized subject's performance on any particular trial is governed by the most strongly activated percept-action node association. The hippocampal deficit in these tasks, then, is attributed to the continued elicitation of the approach response following the first punished trial. With further training, hippocampectomized subjects do acquire the avoidance task, because the association mediating avoidance is strengthened relative to the original association.

A similar interpretation applies to the findings that hippocampectomized subjects are impaired in the acquisition of passive avoidance tasks following the acquisition of a conflicting escape response (Gray, 1982) or of an active avoidance response (Lovely, Grossen, Moot, Bauer and Peterson, 1971; Papsdorf and Woodruff, 1970).

Generally, hippocampectomized subjects are unimpaired in the passive avoidance of an unlearned or spontaneous behavior (e.g., Kimble et al., 1966; Riddel, 1966; Stein and Kirkby, 1967); these findings support the view that prior training in a conflicting response is critical in producing the hippocampal deficit. However, hippocampectomized organisms are sometimes impaired even in the acquisition of an untrained passive avoidance response. For example, hippocampectomized rats with no previous training in a highly motivated approach response were impaired in acquiring the conflicting avoidance response (Isaacson, Olton, Bauer and Swart, 1966). Approach training exacerbated the deficit. The authors argued that "perhaps it is the total behavior tendency toward the response that is the essential factor, and this total tendency could have components from prior training and from motivational circumstances as well" (Isaacson et al., 1966, p. 420). Thus, training and motivational variables may contribute to the relative strength of the associations mediating approach and avoidance behaviors.

This interpretation can be extended to account for the finding that increasing the intensity of the punishing stimulus reduces or overcomes the hippocampal deficit in passive avoidance tasks (Cogan and Reeves, 1979). In this case, motivational variables may accelerate the strengthening of the association mediating the avoidance response.

The hypothesis that hippocampectomized organisms develop conflicting percept-action node associations also accounts for the effects of various training conditions upon their performance in differential reinforcement of low rates schedules.

*Differential Reinforcement of Low Rates (DRL) Schedules*

The performance of hippocampectomized rats on DRL schedules is impaired in a variety of procedures (Gray, 1982). An important variable contributing to the degree of deficit is the training procedure. If pre-trained on a continuous reinforcement (CRF) schedule, hippocampectomized rats are severely impaired in acquiring the DRL schedule (Clark and Isaacson, 1965; Pellegrino and Clapp, 1971; Rickert, Bennett, Anderson, Corbett and Smith, 1973; Schmaltz and Isaacson, 1966). On the other hand, if they are shaped directly on the DRL schedule, the hippocampal deficit is greatly reduced: such subjects are unimpaired relative to controls in the number of reinforcements received per session, although they do perform less efficiently than controls (Schmaltz and Isaacson, 1966; Johnson, Olton, Gage and Jenko, 1977).

A recent series of studies (Rawlins, Winocur and Gray, 1983) has demonstrated that the hippocampectomized rat's deficit is not primarily due to a deficit in performing temporal discriminations. This finding is consistent with the hypothesis (discussed previously in this paper) that the functions of perceptual systems are unimpaired by hippocampectomy.

According to the proposed model of the associative system, the behavior of the hippocampectomized organism in DRL schedules is controlled by two types of stimuli: temporal stimuli and environmental stimuli (the latter include specific cues and chamber stimuli). Various experimental manipulations can alter the relative strength of the percept-action node associations that mediate the control of bar-pressing by these stimuli. Thus, for example, pretraining on CRF increases the control of behavior by chamber stimuli. In this case, subsequent DRL performance is impaired because these stimuli have poor predictive value for the reinforcer—rather, they elicit continuous responding. Furthermore, in accordance with the contiguity principle, the percept-action node association that mediates control of behavior by chamber stimuli continues to be strengthened during DRL training (because chamber stimuli are contiguous with reinforced bar-pressing). Thus, extinction of this association is impaired (see discussion of the associative system in a previous section of this paper; see also, Schmaltz and Isaacson, 1966, p. 181). Consequently, following CRF pre-training, the hippocampectomized organism is impaired in acquiring the conflicting percept-action node association that would mediate the control of DRL performance by temporal stimuli.

When hippocampectomized organisms are shaped directly on DRL, the association between temporal stimuli and bar-pressing is differentially strengthened. However, even in this condition, chamber stimuli maintain some control over behavior—again, because they are contiguous with reinforced responding. Thus, hippocampectomized organisms perform somewhat inefficiently in this condition because chamber stimuli interfere with the control of behavior by temporal stimuli. The findings that hippocampectomized rats are unimpaired in

performance of the cued-DRL procedure (Braggio and Ellen, 1976) are consistent with this account; in this procedure, the most salient environmental stimulus (the cue) does not interfere at all with the control of behavior by temporal stimuli.

*Conditional Discriminations*

Hippocampectomized rats are severely impaired in the acquisition of a conditional discrimination in which the required response is conditional upon deprivation stimuli (Hirsh, Holt and Mosseri, 1978; Hsaio and Isaacson, 1971). For example, in the Hirsh et al. (1978) study, hippocampectomized and control rats were food and water-deprived on alternate days, and were trained in a T-maze having food and water available in opposite arms. The hippocampectomized rats learned to find one reinforcer as quickly as controls; however, they were severely impaired in learning to find the reinforcer appropriate to their deprivation condition.

According to the proposed model, the performance of normal organisms in this task is mediated by propositional chunk nodes coding information regarding which response produces which reinforcer. However, it is also possible that the deprivation stimuli merely elicit the correct response. In an experimental test of this hypothesis, Kendler (1946) demonstrated that normal rats acquire information regarding which response produces which reinforcer even if they have been trained while simultaneously deprived of both food and water. In this condition, deprivational stimuli could not serve as eliciting stimuli for specific responses.

In contrast, the present model proposes that the behavior of hippocampectomized organisms is elicited by available stimuli that are associated with the reinforced response; including, in this procedure, deprivation stimuli and maze stimuli. However, hippocampectomized organisms may be somewhat impaired in discriminating among deprivation stimuli (Hsaio and Isaacson, 1971), and therefore the percept-action node associations mediating performance of this task should be subject to mutual interference. Furthermore, in the Hirsh et al. (1978) study, the two arms of the maze were not differentially cued, and therefore non-conditional maze stimuli were another potential source of interference.

By this account, hippocampectomized rats should be unimpaired if all available cues, including exteroceptive stimuli, are differentially associated with the reinforced response. In this case, exteroceptive stimuli can serve as eliciting stimuli for behavior. In addition, a source of potential interference is eliminated if all cues redundantly elicit the same reinforced response. Hirsh and his colleagues (Hirsh, Leber and Gillman, 1978) have tested fornix-lesioned rats in such a procedure, and found them to be unimpaired relative to controls.

Unfortunately, however, rats having lesions localized to the hippocampus have not been tested in this procedure.

### Consequences of the Hippocampectomized Organism's Inability to Form Stimulus Complex Nodes

Stimulus complex nodes of the chunking system are storage sites for integrated perceptual information. These chunk nodes mediate performance in classical conditioning tasks by storing CS-US pairs and also (in compound conditioning procedures) by storing concurrent CSs. However, in the hippocampectomized organism, conditioning is not a matter of chunking perceptual information but of forming direct percept-action node associations between nodes representing the CS and the CR.

These models can be applied to account for the behavior of intact and hippocampectomized organisms in blocking and overshadowing tasks.

### Blocking

In blocking procedures, a subject is initially trained with a stimulus ($CS_A$). After conditioning occurs, a redundant element ($CS_B$) is added, and the organism is trained with the new compound stimulus ($CS_{AB}$). When the organism is later tested with each element, conditioning is found to have occurred to $CS_A$ but not to $CS_B$.

However, hippocampectomized organisms do not show this blocking effect; that is, they do not respond differentially to the component CSs in blocking procedures (Rickert, Bennet, Lane and French, 1978; Solomon, 1977). In both of these experiments, control subjects exhibited the usual blocking effects. Furthermore, Rickert et al. (1978) reported that manipulations designed to increase the probability of producing blocking in normals (e.g., overtraining with $CS_A$) were also ineffective when applied to the hippocampectomized subjects.

The role of stimulus complex nodes in mediating the differential control of behavior by the $CS_A$ and the $CS_B$ has been discussed previously in this paper. However, since hippocampectomized organisms are incapable of forming stimulus complex nodes, their behavior in this task (and other conditioning procedures) is mediated by the formation of percept-action node associations. Both $CS_A$ and $CS_B$ occur in contiguity with the reinforced response, and therefore percept nodes for both stimuli are associated with the action node for the CR. Thus, in the hippocampectomized organism, conditioning to $CS_B$ is not blocked by prior training with $CS_A$.

*Overshadowing*

In a variation of the Pavlovian overshadowing procedure, a compound CS includes elements that differ in their predictive value for the occurrence and absence of reinforcement. In normal organisms, conditioning to the less predictive element is overshadowed by the element having greater predictive value.

Recently, the performance of hippocampectomized and control rats was compared in such a procedure (Rickert, Lorden, Dawson, Smyly and Callahan, 1979). A visual cue was paired with each of two auditory cues to form two compound conditioned stimuli which served as the $CS^+$ and the $CS^-$ in a conditioned emotional response (CER) paradigm. When tested with the individual CS elements, the hippocampectomized and control subjects did not differ in their response levels to the predictive elements. However, the level of responding to the non-predictive elements was significantly greater in hippocampectomized rats than controls. Thus, although lesioned subjects performed as well as controls on the discrimination task, their responding to the non-predictive elements of the compound CSs revealed no overshadowing.

The substrates of the normal rat's performance in this overshadowing procedure are two chunk nodes: $CS^+$-US and $CS^-$-no US. The presentation of the predictive elements of the conditioned stimuli activates these nodes differentially. However, they are both activated equally by the non-predictive element (which, in this procedure, was paired with each of the predictive elements equally often). However, it is the relative, not the absolute, level of activation that has important consequences for discrimination responding (Martindale, 1981).

Thus, the differential behavior of intact and lesioned organisms in blocking and overshadowing procedures is consistent with the hypotheses that, in normal organisms, conditioned behavior is mediated by stimulus complex chunk nodes within the chunking system, and that, following hippocampectomy, acquisition of classical conditioning tasks is mediated by the associative system. In the following section, the limited ability of hippocampectomized organisms in complex maze tasks also is attributed to their failure to form stimulus complex chunk nodes.

### Consequences of the Hippocampectomized Organism's Inability to Form a Cognitive Map

The processing of spatial information to form place nodes, and the organization of place nodes into a coherent body of spatial information—the cognitive map—is one of the functions of the hippocampal chunking process. According to the proposed model, hippocampectomized organisms are incapable of forming new place nodes, and of incorporating them into cognitive maps. Therefore, they should be severely impaired in the acquisition of spatial tasks. On the

other hand, hippocampectomized organisms should be capable of simple stimulus discriminations and therefore should be capable of acquiring "spatial" tasks that involve learning to approach a specific cue or set of cues. Such behavior could be mediated by direct percept-action node associations.

*Acquisition of Complex Spatial Tasks*

Evidence that hippocampectomized organisms are severely impaired in the post-operative acquisition of spatial tasks is unequivocal (e.g., Harley, 1979; Jarrard, 1978; Morris, Garrud, Rawlins and O'Keefe, 1982).

This deficit is mitigated by cuing. If the organism can perform a "spatial" task by acquiring a simple association between a cue and an approach response, they are unimpaired in task acquisition (Ellen and Bate, 1970; Leaton, 1969; Morris et al., 1982; Nadel and MacDonald, 1980; Winocur, 1982; Winocur and Breckenridge, 1973). Perhaps the clearest example of the differential effects of cuing upon the performance of hippocampectomized organisms has been obtained in the water-maze task designed by Morris (1981). In this task, rats learn to swim to either a submerged hidden platform (place condition), or to a protruding escape platform (cue condition). Normal rats in either condition quickly learn to approach the platform from a distant starting point. Apparently, they use cues that are distal to the platform to aid their performance. Hippocampectomized rats are severely impaired in the place condition, but perform as well as normals in the cue condition (Morris et al., 1982). Transfer tests confirmed the interpretation that hippocampectomized rats failed to acquire spatial information in these tasks.

*Retention of Pre-operatively Acquired Spatial Tasks*

According to the proposed model, pre-operatively consolidated cognitive maps should be spared by hippocampectomy. However, the extant literature does not permit a definitive evaluation of this hypothesis, because there is no clear-cut method of determining whether information is or is not completely consolidated. Furthermore, experiments designed to test retention of pre-operative learning have produced contradictory results; in some such paradigms, retention is spared (e.g., Harley, 1979); in others it is not (e.g., Jarrard, 1983). These contradictory findings may be a consequence of factors affecting consolidation (Squire, Cohen and Nadel, 1983; Wickelgren, 1979). However, within-experiment comparisons are necessary to test this hypothesis.

*Utilization of the Pre-operatively Stored Cognitive Map*

Hippocampectomized rats are generally impaired in the performance of pre-operatively acquired spatial working-memory tasks (Olton, Becker and

Handelmann, 1979). In such tasks, rats are required to enter each arm of a radial maze once and only once. To avoid re-entries (errors), rats must retain, for the duration of a trial, information regarding which arms have already been entered.

According to the proposed model, this task is mediated by the temporary activation of place nodes representing the recently entered arms. If the pre-operatively formed map is incompletely consolidated: that is, if hippocampal afferents to the chunk node have been prematurely removed (by hippocampectomy), then this temporary activation may be impaired (cf., Squire, Cohen and Nadel, 1983).

Interestingly, the deficit of hippocampectomized rats in this task is alleviated if they are pre-operatively trained on a maze in which each arm is saliently cued. This finding may be accounted for if it is assumed that a cognitive map representing the conspicuously cued maze is more rapidly consolidated than one representing the standard radial arm maze (in which the various arms are not specifically cued).

These proposals can be applied to account for some counter-intuitive findings reported by Winocur (1982): that rats pre-operatively trained in a standard radial arm maze were impaired in utilizing salient intra-maze cues that were added to the maze post-operatively. This deficit is not obtained if naive hippocampectomized rats are post-operatively trained with such cues. Therefore, the negative transfer obtained when the cues were added during post-operative testing may be attributed to the reliance of the hippocampectomized rats upon a pre-operatively formed, but incompletely consolidated, cognitive map—and upon their inability to incorporate new information into this cognitive map.

*Alternative Theories of Hippocampal Involvement in Processing of Spatial Information*

In recent years, most experimental tests of the hippocampectomized organism's spatial abilities have been designed to test the theories of O'Keefe and Nadel (1978) and of Olton and his colleagues (Olton, Becker and Handelmann, 1979).

According to Olton et al. (1979), the hippocampal deficit is specifically a working memory deficit. However, many experiments, some of which are reviewed here, have demonstrated that the hippocampal deficit is not specific to working memory procedures; rather, hippocampectomized organisms are impaired in the acquisition of all types of complex spatial tasks (Morris et al., 1982). O'Keefe and Nadel (1978) have proposed that the hippocampus functions as the storage site of the cognitive map, and that the hippocampus is exclusively concerned with this mapping function; it does not process or store non-spatial information.

Investigations of the hippocampectomized organism's ability to retain pre-

operatively acquired complex spatial tasks provide data relevant to the cognitive map theory. As stated above, these experiments have yielded equivocal results. However, in most experiments, there is evidence of some sparing of spatial information following hippocampectomy (e.g., Jarrard and Elmes, 1982, p. 707). Such data is incompatible with the hypothesis that the cognitive map is removed by hippocampectomy. Rather, these data are compatible with the proposed model, which hypothesizes that the chunking system mediates unimpaired performance following hippocampectomy only if the pre-operatively acquired cognitive map has been completely consolidated prior to hippocampectomy, (cf. Squire, Cohen and Nadel, 1983; Wickelgren, 1979).

The hypothesis that the hippocampus is exclusively involved in the processing of spatial information has been specifically tested in a number of studies (e.g., J.W. Moore, 1979; Solomon, 1977, 1979). Disconfirming evidence has been obtained in each of the cases. However, a less literal interpretation of the cognitive map theory has been suggested by Nadel and Willner (1980). According to this interpretation, the hippocampus participates in the processing of many types of contextual information systems. These systems organize environmental data to include information regarding the spatial, temporal, or causal *relations* among this data (cf. Nadel, 1981; Nadel et al., 1984). The Nadel and Willner (1980) hypothesis of hippocampal function is compatible with the present model. However, neither of these views address the issue of the mechanisms for the encoding and storage of relational information; in my opinion, this issue is one of the more important questions that both theories leave open.

## Conclusion

The model proposed here accounts for the pattern of spared learning and amnesic deficits that is observed in hippocampectomized human and non-human mammals. According to the model, hierarchical perceptual and motor systems and their interactions are entirely spared by hippocampectomy. The proposed systems are applied to account for the spared capacity of bitemporal amnesiacs to acquire complex skills. In addition, a system of direct interconnections between the systems is proposed to account for the amnesiac's spared capacity for simple associative learning.

Furthermore, the model proposes that the hippocampus is critically involved in a process of storing and consolidating integrated units of cognitive information, including propositional and complex spatial information. By this view, the amnesic deficit of hippocampectomized organisms includes an inability to acquire information regarding the contingencies of their behavior and an inability to acquire cognitive maps. The proposed chunking systems endow organisms having hippocampi with the capacity for far more complex systems of information storage, and more flexible access to that information, than can be

achieved by organisms relying on the proposed associative system. Thus the different capabilities of the proposed associative and cognitive systems are analyzed here and applied to account for the behavior of hippocampectomized organisms in a variety of behavioral paradigms.

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