

PROCESSES OF ANIMAL MEMORY: EXPERIMENTAL ANALYSES AND ANATOMICAL AND ECOLOGICAL THEORIES

Introduction

The simplest theoretical issue is whether “working memory” processes can be distinguished from mechanisms of response-habit learning and Pavlovian conditioning.

It must be pointed out that the term “memory” is often applied to all effects of previous experience on animal behaviour including the most basic forms of Pavlovian and Thorndikean conditioning (e.g. Kandel & Pittenger, 1999; Kandel, 2001). Distinctions can be drawn however between, for instance, transient sensory buffers; automatic associations; motor skills and response habits; long-term acquired knowledge (as in cognitive maps of local environments) and working memory systems (e.g. Roberts 1998). It has often been emphasised that in many forms of human amnesia, various kinds of perceptual and motor skill learning remains possible (Squire, 1992; Woodruff-Pak, 1993; Gabrieli *et al*, 1995; McKenna & Gerhand, 2002; Hikosaka *et al*, 2002). This suggests that the conditioning process is anatomically separate from other kinds of human memory, and there is evidence to support this from the use of methods in which brain activity is mapped or scanned during the performance of various cognitive tasks (e.g. Esteves *et al*, 1994; Bao *et al*, 2002; Courtney *et al*, 1998). There is also a measure of agreement that in human subjects it is possible to distinguish *implicit* (nonconscious) from explicit learning (e.g. Berry, 1994; Seger, 1994, Persaud *et al*, 2006) and *declarative* (verbally accessible) from non-declarative memory (Green and Woodruff-Pak, 1997; Squire and Zola, 1996; Eichenbaum, 1997, 2000; Poldrack & Packard, 2003: see also Brewin, 2001 in week 7 and Squire and Zola, 1996 and p. 20 of this handout).

There are several particular kinds of behavioural experiment which have been used to support the concept of “*working memory*” in animals as something separate from the minimal associations necessary for basic conditioning in animal learning. Some of these are kinds of experiment are discussed briefly below.

In a change in terminology the data from same general kinds of experiments have recently been discussed as providing evidence for animal models of “*episodic memory*” (Aggleton and Brown, 1999; Griffiths, Dickinson and Clayton, 1999, Suzuki and Clayton, 2000, Morris, 2001, Tulving, 2002; Eacott *et al*, 2005; Babb & Crystal, 2006 – “*declarative memory system*” is also used the same context: Eichenbaum, 1997, 2000).

The general conclusion is that there are distinctions to be drawn between memory for recent events and the associative learning of skills and habits, and that some (but not all) aspects of this distinction apply to both human and animal memory (Kesner & Hopkins, 2006; Eichenbaum, 1997, 2000; Manns & Eichenbaum, 2006; Courtney *et al*, 1998; Suzuki and Clayton, 2000; Morris, 2001; Poldrack & Packard, 2003; Wishaw & Wallace, 2003; Pasternak & Greenlee, 2005).

Sample Essay

Discuss experimental evidence and the theoretical background for the distinction between memory for recent events and response learning in animal behaviour.

Working memory and the radial maze

Olton and Samuelson (1976) introduced a technique which appears to test rats’ memories of where they have recently been. On each daily trial animals are placed at the centre of a series of spokes, referred to as “arms” of the maze. A small amount of food is available (out of sight) at the end of each arm. The most efficient strategy would be for a rat to travel down each arm of the maze just once, retrieving all the available food with the minimum distance travelled. This is indeed the strategy adopted: Olton and Samuelson (1976) found that, after 40 trials, rats chose on average 7.5 different

arms of the possible 8 arms of the maze in their first 8 choices. Control experiments established that the animals were not using odour cues to accomplish this efficient strategy. (Rats continue to behave as though they are choosing different geographical places when they are confined to the centre of the maze after returning from each choice, under conditions which allow the experimenters to swap visited and un-visited arms between choices: Olton and Collison, 1979).

This and other evidence suggests that the animals use fairly distant landmarks (“extra-maze cues”) to distinguish between different parts of the maze, and either remember the places they have been in an overall “cognitive map” of the maze, or have memories organised like “lists” of individual already visited places (Brown, 1992).

The use of radial (and other) mazes allows a distinction to be made between “reference memory” and “working memory”. (e.g. Olton, 1979). Reference memory applies to relatively permanent features of the environment, such as the location of the single goal in a conventional maze, or the position of rewarded arms in a radial maze where only half of the arms are baited each day (the same ones each time: Olton and Pappas, 1979). “Working memory” applies to the mechanism that enables a rat not to revisit arms already visited on a particular day. This form of memory is often linked to the functioning of the hippocampal system in both humans and animals (Scoville and Milner, 1957; Kesner, 1990; Bunsey and Eichenbaum, 1996; Eichenbaum, 1997, 2000; Morris, 2001).

It has been reported that children under the age of 7 perform poorly when tested in a suitably scaled up radial maze, the conclusion being drawn that human brain systems required for spatial memory of this kind are not fully developed until approximately 7 years of age. (Overman *et al*, 1996).

Spatial memory not involving food rewards can be tested with *submerged platform tests*: rats placed in a large tank learn to swim to the location of an invisible platform from variable starting positions, and can learn to make few errors after the first trial when the platform is moved to a different position each day (also called the *Morris water maze*: Morris *et al*, 1982; Gerlai *et al.*, 2002; Morris, 2001.)

Delayed Response Methods

Hunter (1913) tested various species in experiments in which a correct choice between a number of doors was indicated by a brief light above it, animals not being allowed to make the choice until a few seconds time later, and concluded that both rats and dogs solved this problem by maintaining bodily orientation (“pointing”) to the correct direction. However, when animals are shown food in a particular location, they may successfully find it after delays long enough to preclude this peripheral mechanism (Menzel, 1973; see Walker, 1985).

The Delayed-Matching-to-Sample Technique (DMTS)

A widely used experimental method also precludes the use of response perseveration as a mechanism, since it requires some form of memory of the properties of recent stimuli. Usually there is a 3-part visual display. On a central screen a “sample” stimulus is presented (animals being typically required to make an unrewarded response to the sample to ensure it has been noticed). There is then a delay period, which may be variable, before two different “choice” stimuli are presented at the same time on the outside screens, only one being the same as the most recent sample, the subjects being rewarded only if they choose this one. Since the sample is varied from trial, as is also the location, left or right, of the subsequent correct choice, successful performance must be interpreted as due to some kind of transient memory for the sample. The simplest theories propose that “stimulus traces” of the sample, which gradually decay, are used to direct choices, and in many experiments performance declines rapidly with delays longer than a few seconds (Roberts and Grant, 1976; D’Amato and Cox, 1976).

Such theories need to be elaborated however in order to account for proactive and retroactive interference effects (e.g. Overman and Doty, 1980), and superior performance for “surprising” (rare) samples (Lieberman, 2000; p. 380). These results suggest that what is remembered is not a passive

sensory trace of the sample but a more active process. (See Morimura and Matsuzawa, 2001; Hampton, 2001)

A further result which can be obtained with this technique is the *Serial Position Effect* well known from studies of human memory. This is possible because animals can be trained to observe “lists” of samples (e.g. 10 pictures of human artifacts) before a delay, a choice being then presented between one item which was on the most recent list, and one which wasn't (Sands and Wright, 1980; Wright *et al.*, 1984; Castro and Larsen, 1992; Wright, 2002).

Naturalistic experiments on finding stored food.

It is difficult to ascribe an ecological function to the serial position effect obtained in memory for lists of objects, although it may reflect the operation of generally useful memory mechanisms. On the other hand it is possible to observe performance indicative of memory mechanisms which may be highly specialized in species which under natural conditions hoard food in multiple locations.

Textbooks on animal behaviour tend to suggest that squirrels find hoarded food by using their sense of smell, but it is an important aspect of their foraging (Wauters *et al.*, 1995) and there are one or two suggestions that their visual spatial sense is also important in foraging (Devenport *et al.*, 2000; Jacobs and Shiflett, 1999) and mate finding (Schwagmeyer *et al.*, 1998).

By contrast there is a very extensive literature on the importance of visual memory for the retrieval of hoarded food in several bird species. Shettleworth and Krebs (1982) studied the behaviour of marsh tits in an large aviary in which old tree branches had a total of 97 holes drilled in them, covered with cloth flaps. Birds accustomed to the aviary but kept elsewhere were placed in it with a bowl of hemp seeds available, and allowed to store 12 of the seeds in hiding places they selected, which took 7 or 8 minutes. They were then removed from the aviary for 2 or 3 hours, and returned to it with no food available apart from the 12 seeds they had stored. The average performance of four birds each given a 12 minute recovery test of this kind was 8 out of the 12 seeds recovered, from inspections of 30 of the 97 holes. On average, 5 out of the first 10 holes inspected contained seeds. Clearly this performance is not perfect, but it is very substantially better than chance.

Observations of Clark's Nutcracker (a North American corvid — crow-like bird) suggests that an individual bird may store up to 30,000 pine nuts in 2,500 locations during the autumn, returning to these locations throughout the winter, and in some cases much later in the following year. Experiments on captive birds of these species indicated that non-local landmarks are used in coding the location of food-stores, since they made systematic errors if obvious features of the test environment, such as logs or large stones, were moved during the retention interval (Balda and Turek, 1984; Kamil and Balda, 1985; Gouldbeierle and Kamil, 1996, Bednekoff and Balda, 1996). Laboratory experiments on scrub jays (summarised by Griffiths *et al.*, 1999; see also Clayton *et al.*, 2001; 2003 and Dally *et al.*, 2006) suggest that they remember “when” and “what” as well as “where” in the context of food storing episodes.

The theoretical issue of the role of the hippocampus

Experiments using all the above behavioural tests, and neuroanatomical surveys, have been performed to investigate the role of the hippocampus in animal memory. As hippocampal damage has long been identified with deficits in some kinds of memory in humans (Scoville and Milner, 1957; Woodruff-Pak, 1993) the analogy between human and animal memory is strengthened if specific deficits on memory related tasks can be demonstrated.

Large numbers of experiments on a variety of tasks show behavioural deficits as a consequence of damage to the hippocampal system. The dispute between those who have examined this data is whether the deficits arise from interference with storage of geographical information (O'Keefe and Nadel, 1978; Lever *et al.*, 2002) or whether they arise from impairments of a domain-neutral working memory system (Olton, 1979; Eichenbaum, 1997, 2000). The dispute is difficult to resolve, because so many of the tasks used, especially with rats, have a spatial component. However, the two possibilities are not mutually exclusive (Kesner, 1990). The fact that performance impairments are found with tasks

which lack an obvious geographical component is compatible with the position that the hippocampal formation in most species codes both spatial and temporal aspects of recent events (Kesner, 1990; Busner and Eichenbaum, 1996; Eichenbaum, 1997, 2003; Furusawa et al., 2006). Although O'Keefe (1999) continues to maintain the position that the hippocampus should be regarded solely as a cognitive map, at least in rats, most discussions of the human hippocampus assume that it has more varied functions: Manns et al., 2003; Eichenbaum, 1997, 2000, 2003; Fortin et al., 2002, 2004).

Anatomical and ecological issues in theories of animal memory are combined in studies which examine the role of the hippocampus in species with specialized memory functions. Sherry *et al* (1989), Krebs *et al* (1989) and Healy and Krebs (1993) concluded that the relative *size* of the hippocampal complex is larger in food-storing birds than in comparison species (supported by Maguire et al. 2000, Shors et al. 2001 Clayton, 2001, Suzuki & Clayton, 2001, Lucas et al., 2004 and Healy et al., 2005 but contested by Bolhuis & Macphail, 2001 and Brodin and Lundborg, 2003). Sherry and Vaccarino (1989) found that hippocampal lesions impaired birds' abilities to recover food from caches, without impairing recovery of food from sites labelled with distinctive cues. While the literature on homing in pigeons lacks a clear consensus, there have been suggestions (e.g. Gagliardo *et al*, 1999; 2002) that the hippocampus has an important role in some aspects of this complex geographic skill and in particular for the recognition of visual landmarks.

Conclusions

- Several sources of evidence indicate that animals may make use of memory processes which involve temporary storage of recent information, which are *not* necessarily tied to any given response output and which therefore can be distinguished from response skills, impulses or habits. Memory for the presence or absence of food items at certain spatial locations is a significant example, but other procedures, such as Delayed Matching to Sample, show temporary memories for non-spatial features of recent stimuli (see also Hampton, 2001, on p. 19 of the handout).
- Memory about food sources would have obvious functional value for the achievement of optimum foraging strategies in many species, and the ability of individuals in food-storing species to find food they have hidden themselves has been subjected to experimental tests.
- Considerable attention has been paid to the importance of the hippocampal formation for performance of tasks intended to tap working memory, and although there is disagreement about its precise function, in particular the degree to which it is specialized for spatial information, there is some degree of consensus that this brain structure "plays an important role in mediating mnemonic functions" and that "there are significant parallels across species" in this (Kesner, 1990; p.200; see also Squire, 1992; Eichenbaum, 1997, 2004; Maguire *et al*, 2000; Morris, 2001; O'Reilly & Norman, 2002; Poldrack & Packard, 2003; Ekstrom et al., 2003; Ferbinteanu & Shapiro, 2003; Hori et al., 2005; Manns & Eichenbaum, 2006; Suzuki, 2006).

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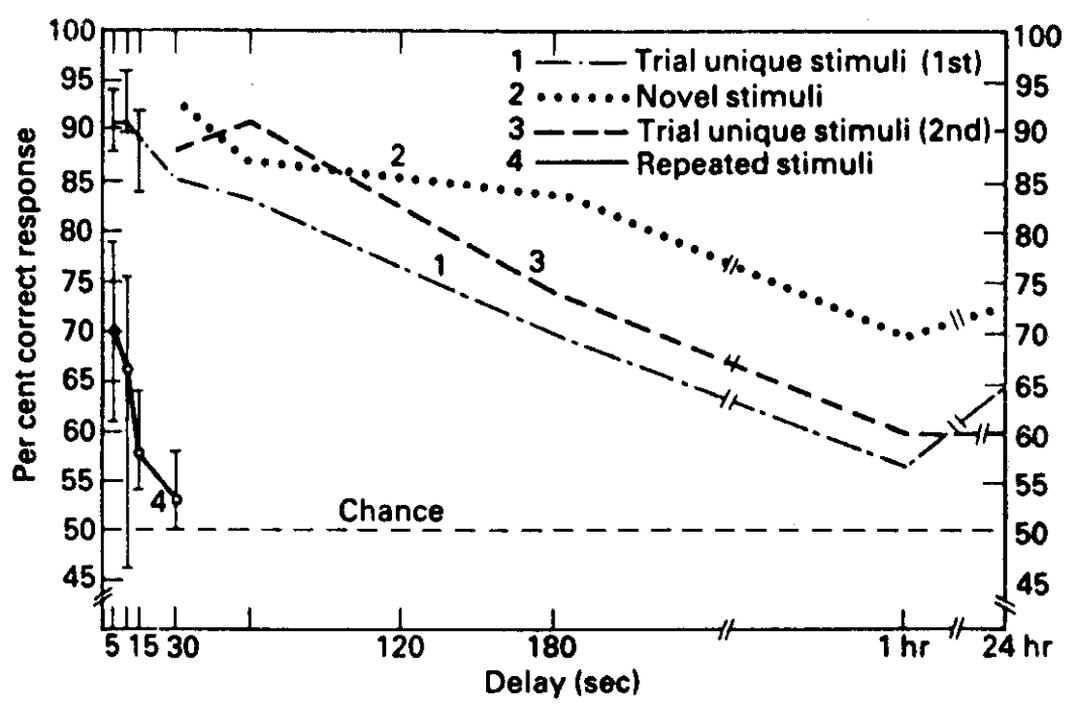


Figure 9.3 Short-term visual memory in monkeys as a function of delay and interference.

If only one pair of coloured slides is presented to monkeys, and they are repeatedly required to choose whichever one of these two had just been shown to them a few seconds earlier, their choice accuracy drops precipitously after 10 seconds' delay. However, if slides were used only once per day ('trial unique'), or if the correct choice was always a novel slide, then 'short-term' memory could be measured in hours instead of seconds. See text. After Overman and Doty (1980).

other extreme, the same monkeys had previously been tested under the constraint that every trial began with a novel slide, never seen by the animal before, and after the delay interval there was a choice between this once-seen slide and an alternative never-seen picture (most slides were of human artifacts: a shoe, a mug, spectacles and so on). Here, by contrast, performance was relatively resistant to temporal delays, even when the animals were removed from the apparatus after seeing the sample, and returned to it an hour or a day later (Figure 9.3). Only slightly less resistant was the monkeys' initial performance with a set of 100 slides used repeatedly for several days, but with each pair of slides being used only once a day. This would appear to be conclusive evidence that

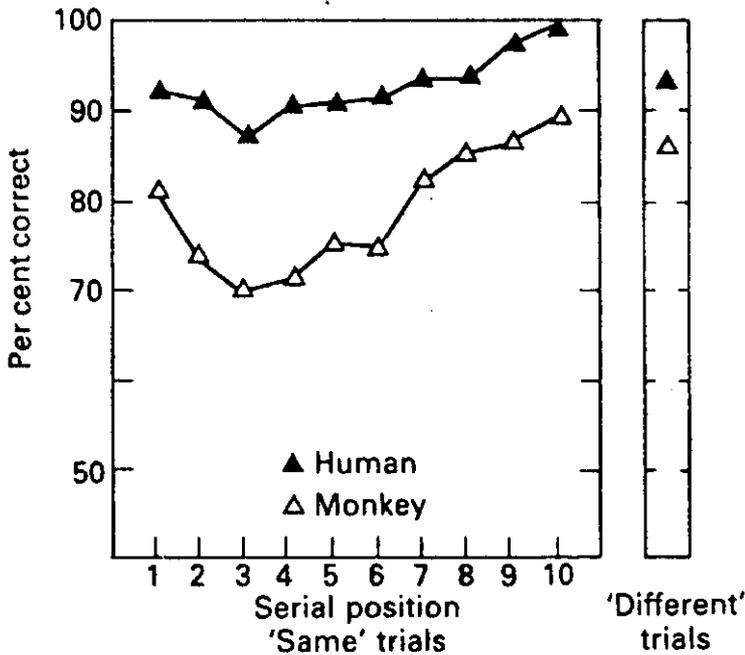


Figure 9.4 *The serial position effect in a monkey's memory for lists.*

See text. After Sands and Wright (1980b).

correct response was to move a lever to the right, and if, alternatively, the slides were obviously different, the same lever was to be pushed to the left. Various food rewards were given intermittently for correct responses. With sufficient training on this same/different principle, it was possible to move on to what is referred to as 'serial probe recognition', in which a 'list' of 10 slides were shown serially on the top screen, followed by a single slide on the bottom screen, and occasional rewards were obtained by pressing the lever to the right if the bottom slide had appeared on the previous top list, and to the left if it had not. The data resulting from this training are shown in Figure 9.4, along with data obtained from a single human subject performing without any reward or previous experience on the task. A more pronounced bowing of the serial position curve is apparent for the rhesus monkey than for the human subject, due no doubt to the ceiling affect produced by the greater accuracy of the latter. When the list was lengthened to 20 slides, the human and monkey curves became more similar.

Walter (1987)

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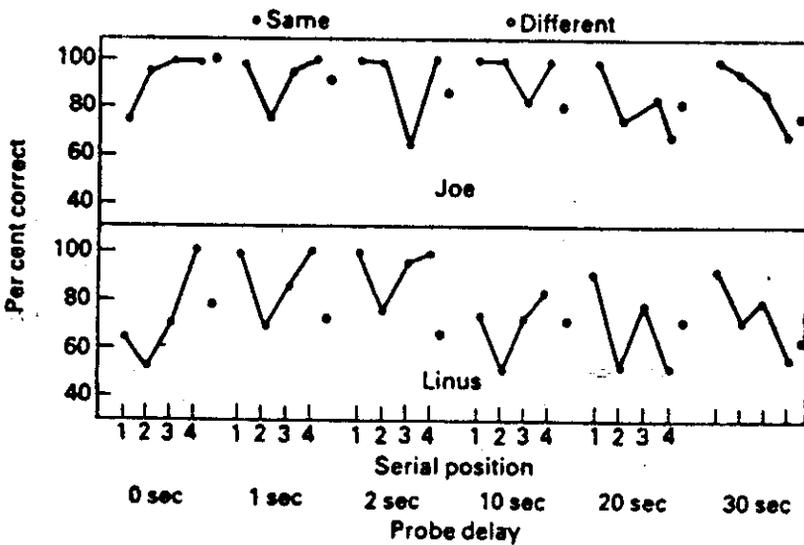
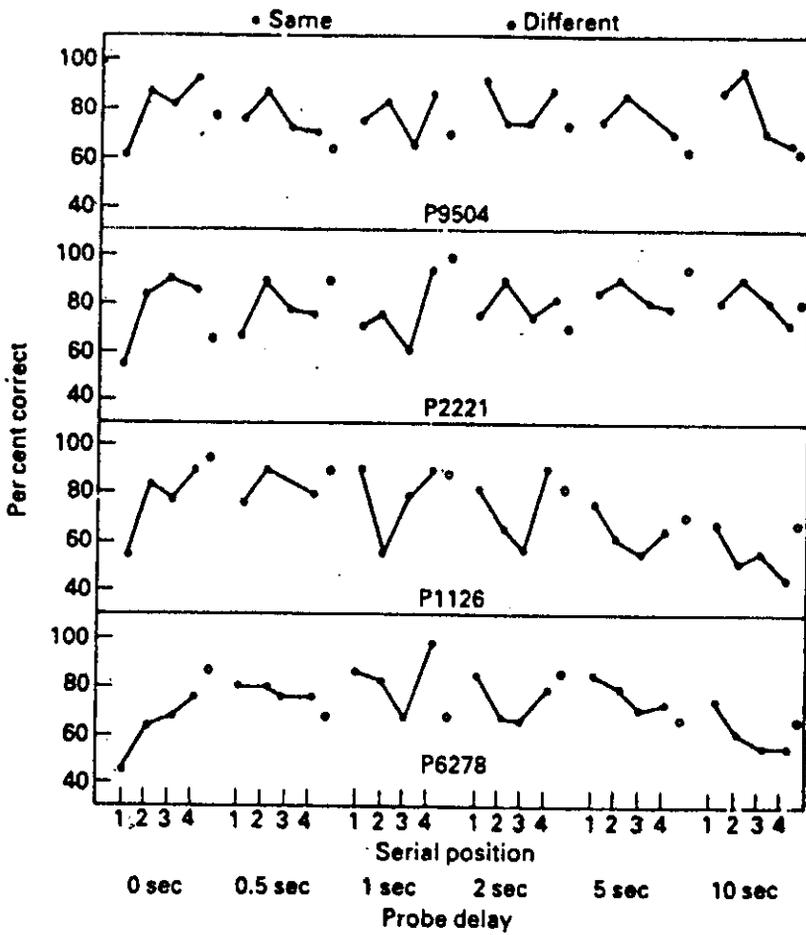


Figure 9.5 *Serial position effect in pigeons and monkeys as a function of probe delay.*

Serial position curves for 4 pigeons (above) and 2 monkeys (below) obtained using the same stimulus materials (coloured slides of objects) in lists of 4, and with various delays intervening between the list and the probe test, at which the animals were required to indicate whether a probe stimulus had been present in the previous list. See text. After Santiago and Wright (1984) and Wright *et al.* (1984a).

Bunsey, M & Eichenbaum, H (1996) Conservation of hippocampal memory function in rats and humans. (see below for [abstract](#))

“If cocoa goes with coffee and coffee goes with onion, does cocoa go with onion?”

<i>First Training (of rats: all discriminations for smell)</i>				
Cocoa	Coffee ✓ Salt	AND	Turmeric	Coffee Salt ✓
<i>Second Training</i>				
Coffee	Onion ✓ Nutmeg	AND	Salt	Onion Nutmeg ✓
<i>Probe Test</i>				
Cocoa	Onion Nutmeg	AND	Turmeric	Onion Nutmeg

Abstract

THE hippocampus is critical to declarative memory in humans(1). This kind of memory involves associations among items or events that can be accessed flexibly to guide memory expression in various and even new situations(2-4). In animals, there has been controversy about whether the hippocampus is specialized for spatial memory(5,6) or whether it mediates a general memory function(3,4), as it does in humans. To address this issue we trained normal rats and rats with hippocampal damage on nonspatial stimulus-stimulus associations, then probed the nature of their memory representations. We report here that normal rats demonstrated two forms of flexible memory expression, transitivity, the ability to judge inferentially across stimulus pairs that share a common element, and symmetry, the ability to associate paired elements presented in the reverse of training order. Rats with neurotoxic damage limited to the hippocampus demonstrated neither form of flexible expression, indicating that non-spatial declarative processing depends specifically on the hippocampus in animals as it does in humans.

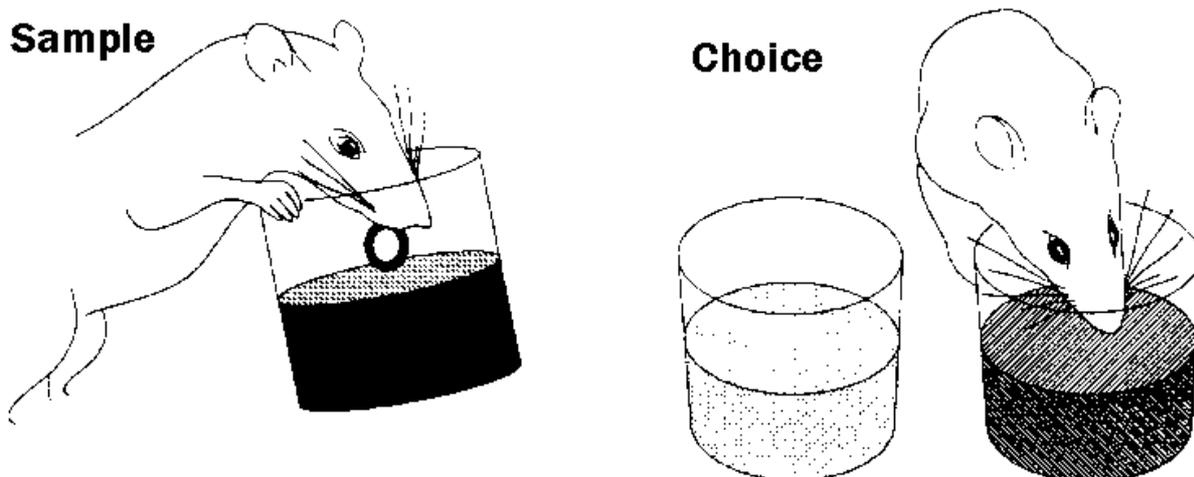


FIG. 1 Training on odour-odour paired associates. Each training trial consisted of two phases. In the sampling phase, the subject was presented with a cup containing a scented mixture of sand and ground rat chow with a buried reward. In the subsequent choice phase, two scented choices were presented. Both the choice items involved odours that were different from the sample, but which of them contained the bait depended on the odour of the sample. All training and tested took place in the home cage. The reward was a piece of buried sweet cereal.

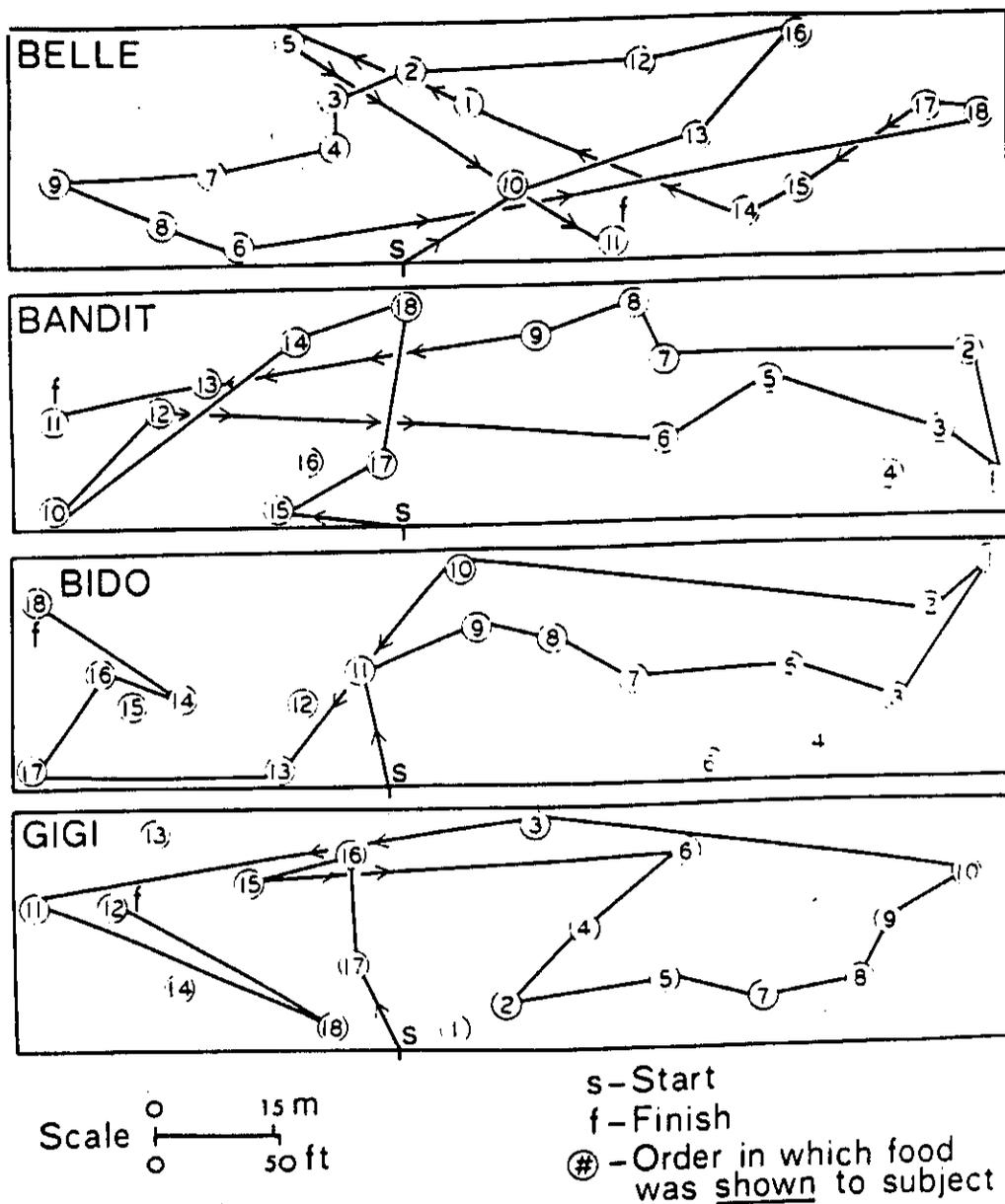


FIG. 11. Maps showing each test animal's performance on the trial (out of four) on which it found the largest number of foods. The connecting lines give an exact picture of the order in which the various places were searched and a rough idea of the animal's general travel routes. Where the line touches a point, that place was searched.

fruits and the itinerary to vegetables are considered separately, each showed a reasonable least-distance pattern.

It is unlikely that all 18 places were taken into account simultaneously at all times throughout a trial in these two experiments. On several occasions, a test

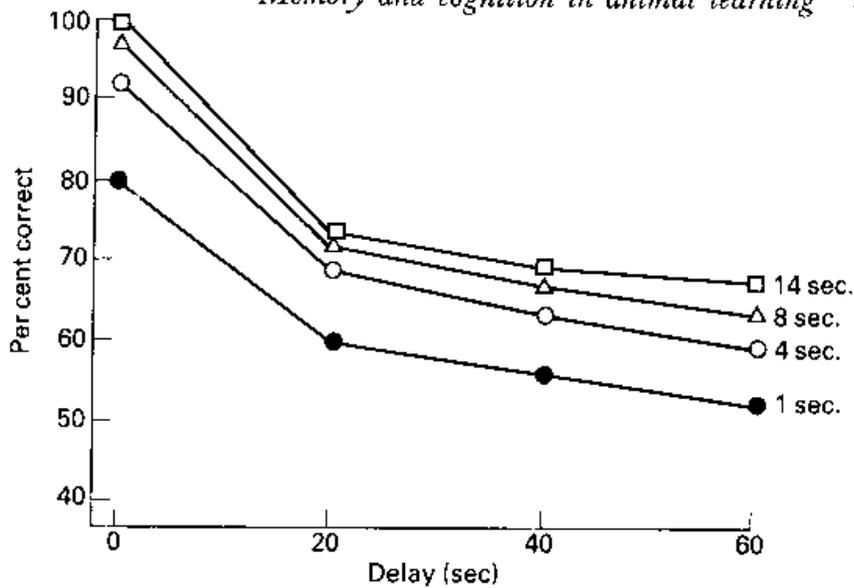


Figure 9.2 Short-term memory in pigeons as a function of recency and stimulus duration.

Per cent correct responses when pigeons were required to choose whichever of 2 colours had been presented at the beginning of a delay period. The length of the delay period is given on the horizontal axis and the duration of the stimulus presentation before the delay is indicated on the figure. See text. After Grant (1976).

In Walker (1987)

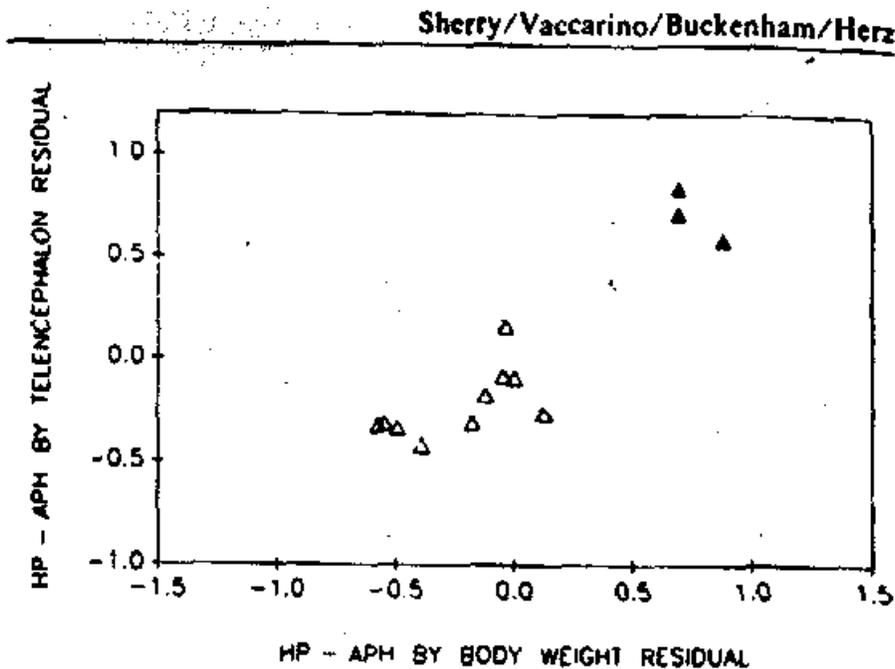


Fig. 5. Residuals of the regression between Hp-APH volume and telencephalon volume plotted against residuals of the regression between Hp-APH volume and body weight. \blacktriangle = Food-storing subfamilies; \triangle = non-food-storing subfamilies.

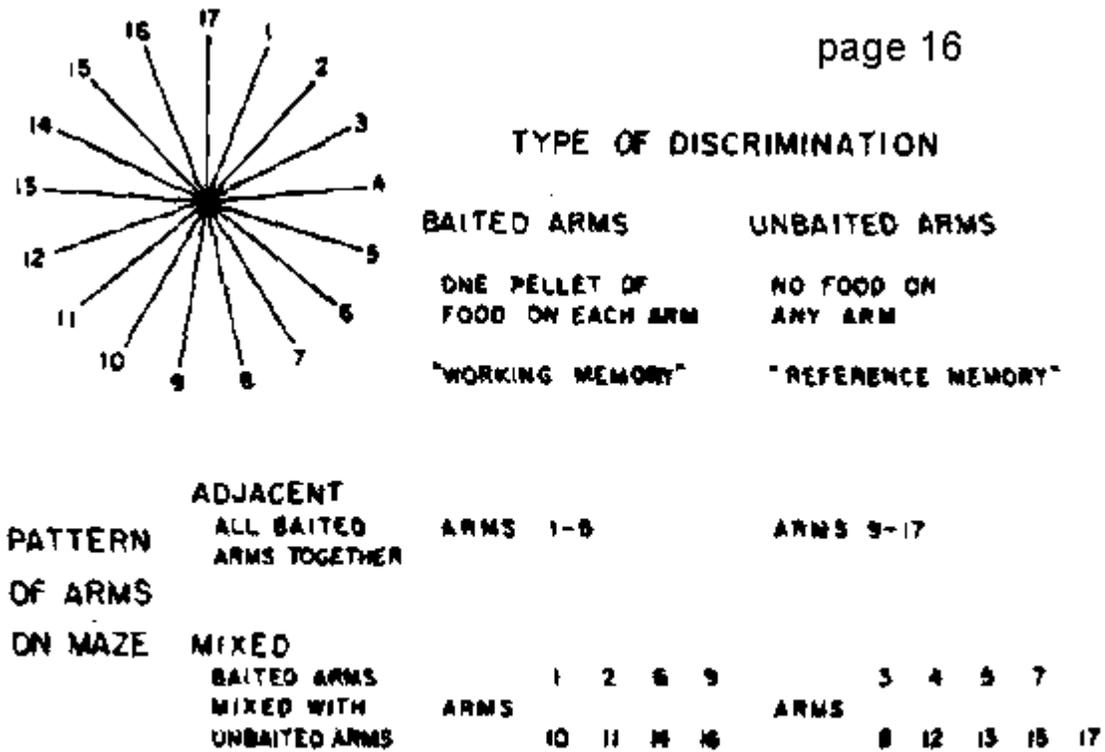


FIG. 1. A summary of the experimental design. For further explanation, see text.

After initial training, rats were tested once a day, 5 days a week. At the beginning of each test, the rat was placed in the central platform with all the guillotine doors closed. All the doors were then raised simultaneously and the rat allowed to choose an arm. When the rat returned to the central platform, all the guillotine doors were lowered again, confining the rat for 10 seconds, after which the doors were raised again. This procedure continued until all 8 arms had been chosen, or until 15 minutes had elapsed.

www.online version of this paper.

QUOTE from Morris, R. G. M. (2001).

“the view taken here is that the hippocampus is a system for the automatic recording of attended experience that enables the encoding, storage and private recollection of experience in a form that would be advantageous to an animal but cannot yet be communicated to another.”

Clayton, NS, Dickinson, A (1999) Memory for the content of caches by scrub jays (*Aphelocoma coerulescens*). *Journal of Experimental Psychology-Animal Behavior Processes*, Vol.25, No.1, Pp.82-91.

To test whether scrub jays (*Aphelocoma coerulescens*) remember the contents of food caches, in Experiment 1 birds cached peanuts and kibbles in two distinct caching trays and recovered them 4 or 172 hr later. The relative incentive value of the foods was manipulated by prefeeding one of the foods immediately before cache recovery. Birds preferentially searched for non-prefed food caches even when the caches had been pilfered prior to the recovery test. In Experiment 2, birds cached both foods in different sites within each tray, recovering peanuts from one tray and kibbles from the other tray 3 hr later. After prefeeding with one food, birds preferentially searched tray sites in which they had cached but not retrieved the non-prefed food. Thus jays remember the specific foods they cache and recover by a mnemonic process that cannot be explained in terms of simple associations between the foods and their cache locations.

Fortin, N. J., Agster, K. L., & Eichenbaum, H. B. (2002). Critical role of the hippocampus in memory for sequences of events. *Nature Neuroscience*, 5(5), 458-462.

Recent models of hippocampal function emphasize the potential role of this brain structure in encoding and retrieving sequences of events that compose episodic memories. Here we show that hippocampal lesions produce a severe and selective impairment in the capacity of rats to remember the sequential ordering of a series of odors, despite an intact capacity to recognize odors that recently occurred. These findings support the hypothesis that hippocampal networks mediate associations between sequential events that constitute elements of an episodic memory.

Healy, S. D., de Kort, S. R., & Clayton, N. S. (2005). The hippocampus, spatial memory and food hoarding: a puzzle revisited. *Trends in Ecology & Evolution*, 20(1), 17-22.

Behavioural ecology assumes that cognitive traits and their underlying neural substrates are shaped by natural selection in much the same way as morphological traits are, resulting in adaptation to the natural environment of the species concerned. Recently, however, the 'neuroecology' approach of attempting to gain insight into brain structure and function by testing predictions about variation in brain structure based on knowledge of the lifestyle of the animal has been criticized on the grounds that such an adaptationist view cannot provide insight into the underlying mechanisms. Furthermore, the criticism has focussed on attempts to use variation in demand for spatial memory and in hippocampal size as a basis for predicting variation in cognitive abilities. Here, we revisit this critique against the field of so-called 'neuroecology' and argue that using knowledge of the natural history of animals has led to a better understanding of the interspecific variation in spatial abilities and hippocampal size, and to the generation of novel hypotheses and predictions.

Kandel, E. R. (2001). Neuroscience - The molecular biology of memory storage: A dialogue between genes and synapses. *Science*, 294(5544), 1030-1038.

One of the most remarkable aspects of an animal's behavior is the ability to modify that behavior by learning, an ability that reaches its highest form in human beings. For me, learning and memory have proven to be endlessly fascinating mental processes because they address one of the fundamental features of human activity: our ability to acquire new ideas from experience and to retain these ideas over time in memory. Moreover, unlike other mental processes such as thought, language, and consciousness, learning seemed from the outset to be readily accessible to cellular and molecular analysis. I, therefore, have been curious to know: What changes in the brain when we learn? And, once something is learned, how is that information retained in the brain? I have tried to address these questions through a reductionist approach that would allow me to investigate elementary forms of learning and memory at a cellular molecular level-as specific molecular activities within identified nerve cells.

McKenna, P., & Gerhand, S. (2002). Preserved semantic learning in an amnesic patient. *Cortex*, 38(1), 37-58.

A case study is reported of an amnesic patient (KN), who displayed an ability to learn a substantial body of new visual and verbal semantic concepts, despite having a severe deficit in episodic memory. In two experiments, using an errorless learning paradigm, he was able to perform at a level close to that of his wife, who served as a control subject. When recall of material was retested after a delay of several months, during which time there were no further learning sessions, his retention was at least as good as, if not better, than that of his wife. This is taken as further evidence for the dissociation of semantic and episodic processes in amnesia. It also provides further evidence for the role of "errorless learning" in efficient acquisition of new facts in amnesia.

Morimura, N., & Matsuzawa, T. (2001). Memory of movies by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 115(2), 152-158.

How do animals remember what they see in daily life? The processes involved in remembering such visual information may be similar to those used in interpreting moving images on a monitor. In Experiment 1, 4 adult chimpanzees (*Pan troglodytes*) were required to discriminate between movies using a movie-to-movie matching-to-sample task. All chimpanzees demonstrated the ability to discriminate movies from the very 1st session onward. In Experiment 2, the ability to retain a movie was investigated through a matching-to-sample task using movie stills. To test which characteristics of movies are relevant to memory, the authors compared 2 conditions. In the continuous condition, the scenes comprising the movie progressed gradually, whereas in the discrete condition, the authors introduced a sudden change from one scene to another. Chimpanzees showed a recency effect only in the discrete condition, suggesting that composition and temporal order of scenes were used to remember the movies.

Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L., & Fried, I. (2003). Cellular networks underlying human spatial navigation. *Nature*, 425(6954), 184-187.

Place cells of the rodent hippocampus constitute one of the most striking examples of a correlation between neuronal activity and complex behaviour in mammals(1,2). These cells increase their firing rates when the animal traverses specific regions of its surroundings, providing a context-dependent map of the environment(3-5). Neuroimaging studies implicate the hippocampus and the parahippocampal region in human navigation(6-8). However, these regions also respond selectively to visual stimuli(9-13). It thus remains unclear whether rodent place coding has a homologue in humans or whether human navigation is driven by a different, visually based neural mechanism. We directly recorded from 317 neurons in the human medial temporal and frontal lobes while subjects explored and navigated a virtual town. Here we present evidence for a neural code of human spatial navigation based on cells that respond at specific spatial locations and cells that respond to views of landmarks. The former are present primarily in the hippocampus, and the latter in the parahippocampal region. Cells throughout the frontal and temporal lobes responded to the subjects' navigational goals and to conjunctions of place, goal and view.

Shors, T. J., Miesegaes, G., Beylin, A., Zhao, M. R., Rydel, T., & Gould, E. (2001). Neurogenesis in the adult is involved in the formation of trace memories. *Nature*, 410(6826), 372-376.

The vertebrate brain continues to produce new neurons throughout life(1-12). In the rat hippocampus, several thousand are produced each day, many of which die within weeks(13). Associative learning can enhance their survival(13,14); however, until now it was unknown whether new neurons are involved in memory formation. Here we show that a substantial reduction in the number of newly generated neurons in the adult rat impairs hippocampal-dependent trace conditioning, a task in which an animal must associate stimuli that are separated in time(15). A similar reduction did not affect learning when the same stimuli are not separated in time, a task that is hippocampal-independent(16,17). The reduction in neurogenesis did not induce death of mature hippocampal neurons or permanently alter neurophysiological properties of the CA1 region, such as long-term potentiation. Moreover, recovery of cell production was associated with the ability to acquire trace memories. These results indicate that newly generated neurons in the adult are not only affected by the formation of a hippocampal-dependent memory(13), but also participate in it.

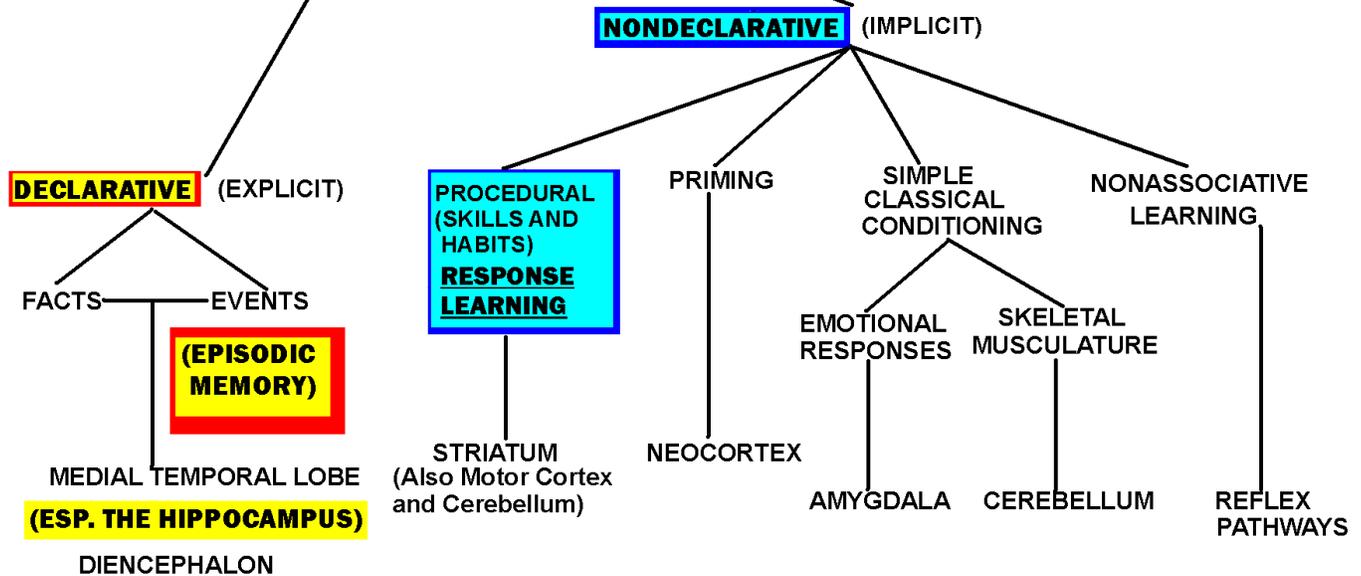
Hampton, R. R. (2001). Rhesus monkeys know when they remember. *Proceedings of the National Academy of Sciences of the United States of America*, 98(9), 5359-5362.

Humans are consciously aware of some memories and can make verbal reports about these memories. Other memories cannot be brought to consciousness, even though they influence behavior. This conspicuous difference in access to memories is central in taxonomies of human memory systems but has been difficult to document in animal studies, suggesting that some forms of memory may be unique to humans. Here I show that rhesus macaque monkeys can report the presence or absence of memory. Although it is probably impossible to document subjective, conscious properties of memory in nonverbal animals, this result objectively demonstrates an important functional parallel with human conscious memory. Animals able to discern the presence and absence of memory should improve accuracy if allowed to decline memory tests when they have forgotten, and should decline tests most frequently when memory is attenuated experimentally. One of two monkeys examined unequivocally met these criteria under all test conditions, whereas the second monkey met them in all but one case. Probe tests were used to rule out "cueing" by a wide variety of environmental and behavioral stimuli, leaving detection of the absence of memory per se as the most likely mechanism underlying the monkeys' abilities to selectively decline memory tests when they had forgotten.

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LONG-TERM MEMORY

(back of handout)



This diagram is after Figure 1 in the article below.

Squire, LR, Zola, SM (1996) Structure and function of declarative and nondeclarative memory-systems. *Proceedings of the National Academy of Sciences of the United States of America*, Vol.93, No.24, Pp.13515-13522.

This article reviews recent studies of memory systems in humans and nonhuman primates. Three major conclusions from recent work are that (i) the capacity for nondeclarative (nonconscious) learning can now be studied in a broad array of tasks that assess classification learning, perceptuomotor skill learning, artificial grammar learning, and prototype abstraction; (ii) cortical areas adjacent to the **hippocampal** formation are an essential part of the medial temporal lobe memory system that supports declarative (conscious) memory; and (iii) in humans, **bilateral damage limited to the hippocampal formation** is nevertheless sufficient to **produce severe anterograde amnesia** and temporally graded retrograde amnesia covering as much as 25 years.

Poldrack, R. A., & Packard, M. G. (2003). Competition among multiple memory systems: converging evidence from animal and human brain studies. *Neuropsychologia*, 41(3), 245-251.

Research of the neurobiological bases of learning and memory suggest that these processes are not unitary in nature, but rather that relatively independent neural systems appear to mediate different types of memory. Neurobiological studies, for instance, have identified separable cognitive or "declarative" and stimulus-response "habit" memory systems that rely upon the medial temporal lobe (e.g. hippocampus) and basal ganglia (e.g. caudate-putamen), respectively. Evidence indicates that multiple memory systems are activated simultaneously and in parallel in various learning tasks, and recent findings suggest that these systems may interact. One form of interaction between medial temporal lobe and basal ganglia memory systems appears competitive in nature, and has been revealed in non-human animal studies in which damage to a given memory system results in enhanced learning. Recent human neuroimaging research has also provided evidence in favor of competition between memory systems. Thus, **converging evidence across species supports the hypothesis of interactive multiple memory systems in the mammalian brain.** Potential neurobiological mechanisms mediating such interactions include direct anatomical projections between the medial temporal lobe and basal ganglia, indirect neuromodulatory influences of other brain structures (e.g. basolateral amygdala) and activity of neocortical brain regions involved in top-down response selection. (C) 2002 Elsevier Science Ltd. All rights reserved.