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The hippocampus as episodic encoder: Does it play tag?

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Rawlins's characterization of the hippocampus as a "high-capacity, immediate-term memory store" captures the essential idea in a number of previous models. For example, Gaffan (1974), Gray (1984), Hirsh (1980), Kesner (Bierley, Kesner & Novak 1983), Olton (Olton, Becker & Handelman 1979), Solomon (1980), and Winocur (1980) all agree that hippocampal animals show memory deficits when required to identify, for whatever reason, one specific event out of a list of recent events. Although these authors disagree on a number of details, Rawlins has identified their models common ground, the core of each model. (It is only fair to note that Gaffan has considerably modified his ideas about the hippocampus; cf. Gaffan, Saunders, Gaffan, Harrison, Shields & Owen 1984.)

Rawlins's target article impelled me to make two points. The first is that our current memory models for intact animals are not adequate to allow detailed descriptions of the function of the hippocampus in animal memory. The second suggests an alternative view of hippocampal function which may, however, be functionally equivalent to Rawlins's model. It is that hippocampal damage disrupts the encoding of events into episodic memory (Tulving 1984), so that these events cannot be discriminated effectively when they are later retrieved to guide choice behavior.

My first point derives from the fact that most of the data Rawlins presents are only vaguely consistent with his model. For example, he correctly stresses the finding that fornix-lesioned monkeys can solve Win-stay/Lose-shift problems but not Win-shift/Lose-stay problems (Section 15; e.g. Gaffan et al. 1984). When I ask myself "How do intact monkeys solve these problems?" I realize that I do not know. I'm not sure anybody does. Despite considerable research on the topic (e.g. Honig 1984; Premack 1983; Roitbalt 1982), we are only beginning to be able to describe the details of how animals encode and represent events in memory, and of how they process these representations. Because I am not sure of the details of the process by which normal animals solve Win-shift/Lose-stay problems, it is difficult to describe precisely how hippocampal lesions influence performance on this task. We are at the point where the distinctions between some of the competing theories of hippocampal function are finer than the distinctions in our memory models for intact animals. Memory models are lagging behind physiological analysis in much the same way that descriptions of behavior have lagged behind physiological interpretations (e.g. Vanderwolf, Kramis, Gillespie & Bland 1975), and possibly for the same reasons.

My second point concerns Rawlins's note (Section 11) that the role of the hippocampus might be to permit rehearsal rather than to act as an intermediate memory store. I would like to suggest

another way in which the hippocampus might function. John Staddon and I (unpublished manuscript, summarized in Staddon, 1983, pp. 376-89) presented a model accounting for animals' behavior on certain spatial memory tasks, such as the radial maze task, delayed and spontaneous alternation and delayed matching-to-sample tasks, in which we claimed that the critical feature in these tasks was a temporal discrimination between specific events. (It is obvious that our model shares characteristics with several of those mentioned above.) WE said that solution of the radial maze problem, for example, requires a spatial code, a temporal code, and a response rule separate from these two codes. A subject entering an arm of the maze would "tag" the spatial code for that arm with a temporal marker and later choose between two arms on the basis of the relative ages of their temporal markers. The particular arm chosen would depend on the response rule specifying the relationship between the temporal markers and behavior. Staddon and I also suggested that sets of spatial codes could be segregated by context, reducing interference between the codes. For example, spatial codes for arms radiating from different choice points (Roberts 1979) or in different rooms (Roberts 1981) might be distinctively labeled by a context tag (cf. Roberts 1984).

Our "temporal model of spatial memory" was not concerned with the functions of the hippocampus, but it offers a third possibility for hippocampal influence on memory processes, i.e. that the hippocampus subserves episodic memory (Tulving 1984) by tagging the representations of specific events with detailed contextual information. Suppose that the hippocampus functions to tag the representations of events (stimuli or responses) with their spatiotemporal context (cf. Hirsh 1980; Solomon 1980; Winocur 1980). Suppose also that such representations are transferred from a limited-capacity, short-term store directly to a large-capacity long-term store, i.e. the hippocampus is not an intermediate-term, high-capacity store. Then the effects of hippocampal lesions would not become evident until the capacity of the short-term store was exceeded (à la Rawlins; since I assume that the few representations in the short-term store are easily discriminated). Only when delay or intervening events have exceeded the short-term memory capacity is it necessary for an animal to retrieve representations from long-term memory in order to, for example, choose between two previously visited maze arms. Animals with hippocampal damage would be expected to have difficulty discriminating the temporal order of events and distinguishing between repeated exposures to the same event (e.g. response, maze arm, object) because the individual episodes would not have been labeled with a contextual tag. This model of the hippocampus as an episodic memory encoder can make all of the predictions made by Rawlins's model without requiring that the hippocampus serve as a memory buffer. I cannot see how to distinguish, empirically, between Rawlins's model and my proposal. Perhaps he can.