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Eichenbaum *et al.* (1994) provide an important and stimulating analysis of many data about the hippocampal memory system. As their title suggests, they identify “two functional components” of this system, and are thus part of a fertile tradition that dichotomizes memory functions into two complementary compartments. Dichotomies such as declarative memory/procedural memory, knowing that/knowing how, taxon/locale, memory/habit have served their creators well. On the other hand, each of these dichotomies fails to handle large sets of data, if only because they do not deal with key learning problems that animals and humans need to solve.

An alternative approach is to develop neural models of how animals and humans learn to rapidly adapt to changing environmental circumstances in real time. Such real time analyses have disclosed concepts and mechanisms that are invisible to descriptive analyses. Real time analyses have hereby suggested how the hippocampal system may interact with several other brain systems, and why it plays multiple roles in recognition memory, attention, cognitive-emotional interactions, adaptive timing, and spatial orientation. Such analyses go beyond the Eichenbaum *et al.* analysis in several respects, and do not support it in some particulars.

One analysis concerns how humans and animals rapidly learn to categorize events and their contexts in real time. This analysis shows how processes of recognition learning, categorization, attention, memory search, expectation, and novelty detection work together to realize object recognition. Interactions between inferotemporal (IT) cortex and hippocampal formation are particularly emphasized. It is suggested how an attentional subsystem carries out the learning of bottom-up recognition categories and top-down expectations by interacting with an orienting subsystem that triggers reset and memory search for new or better categories when an input exemplar is too novel to match an active top-down prototype. The attentional subsystem models part of the Where cortical processing stream that includes IT cortex. The orienting subsystem is interpreted to intersect the hippocampal system. Together these systems are called an Adaptive Resonance Theory, or ART, model. A lesion of the ART model’s orienting subsystem creates a formal memory disorder much like

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the medial temporal amnesia that is caused in animals and patient HM after hippocampal system lesion. See Carpenter and Grossberg (1993) for a recent review and Grossberg (1975, 1982) for development of this hypothesis. Properties of the ART model also clarify how, in Eichenbaum *et al.*'s words, the hippocampal system achieves "flexible expression of memories in novel contexts" and why matching tasks are relevant to hippocampal function, such that hippocampal neurons respond differently to match and non-match conditions (Otto and Eichenbaum, 1992; Riches *et al.*, 1991; Sakurai, 1990). Indeed mismatches within the attentional system trigger memory searches for better recognition categories by activating the orienting subsystem.

These modelling results do not support the Eichenbaum *et al.* claim that "representational properties of the hippocampal system comprise the fundamental characteristics of declarative memory" or that the "hippocampal representation ... reflect[s] ... the abstraction of relevant relations among ... stimuli." In fact, *no* memories are stored within an ART orienting subsystem. Rather, interactions between the orienting and attentional subsystem enable the latter to rapidly and stably learn to categorize new information in a way that is sensitive to environmental relationships. Without the orienting subsystem, these properties are substantially degraded. Carpenter and Grossberg (1993) suggest experiments to test this prediction. Eichenbaum *et al.* seem themselves to be unclear about this point, since they say "whether the hippocampal system actually stores memories remains unclear."

Eichenbaum *et al.* dichotomize the temporal and representational properties of hippocampal memory processing as "orthogonal functional properties". They do not, however, say why a single brain structure should combine these properties, especially if they are "orthogonal". Real-time neural models distinguish these processes mechanistically, but also show how they may be intimately linked. These results clarify how the hippocampal system may mediate tasks like delayed non-match to sample (DNMS) wherein both temporal delays and novelty-based computations are involved.

The larger issues about temporal properties that are treated by the neural models con-

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cern how cognitive-emotional interactions are coordinated, particularly how classical and instrumental conditioning are cognitively modulated and adaptively timed. The basic conditioning model was introduced in Grossberg (1971, 1972a, 1972b, 1975) and elaborated steadily thereafter, as in Grossberg (1987, 1988). This model analyses suggest that (at least) three types of internal representation interact during conditioning: sensory representations S , drive representations D , and motor representations M . The S representations are categorical representations of external events. The D representations are sites where reinforcing and homeostatic cues converge to generate motivational decisions. The M representations control discrete adaptive responses. Three types of learning take place among these representations: $S \rightarrow D$ conditioned reinforcer learning; $D \rightarrow S$ incentive motivational learning; and $S \rightarrow M$ motor learning. Learned $S \rightarrow D \rightarrow S$ positive feedback quickly draws attention to motivationally salient cues and blocks activation of less salient cues via lateral inhibition among the S categories. $D \rightarrow S$ feedback also energizes the release of discrete adaptive $S \rightarrow M$ responses. It was predicted in Grossberg (1971, 1975) that the final common path of the drive representations D , at or after the stage at which motivational decisions are made, intersects or is modulated by the hippocampal formation. This prediction has received several types of experimental support. For example, Thompson *et al.* (1987) have shown that $S \rightarrow D$ “hippocampal” conditioning subserves the conditioned emotional response whereas $S \rightarrow M$ “cerebellar” conditioning subserves the discrete adaptive response, and hippocampal ablation attenuates blocking (Rickert *et al.*, 1978; Solomon, 1977). These properties clarify how “hippocampal system damage can result in either impaired or abnormally strong utilization of contextual cues” due to a failure of blocking combined with a failure of flexible reset and memory search to discover appropriate cue combinations for attentive categorical binding.

Why, though, should it be the hippocampal formation rather than another brain region, that modulates emotional conditioning? Neural models suggest that this is due to the way in which adaptive timing is linked to conditioning, motivated attention, and orienting responses (Grossberg and Merrill, 1992, Grossberg and Schmajuk, 1989). In particular, $S \rightarrow$

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$D \rightarrow S$ feedback can rapidly draw attention to motivationally salient cues, at the same time that inhibition from D to the orienting subsystem inhibits maladaptive orienting responses in response to fluctuating situational cues. Another process is, however, needed to *maintain* attention during the variable delays that are characteristic of task demands. In particular, suppose that an animal inspects a food box right after a signal occurs that predicts food delivery in 6 seconds. Why does not the animal interpret the immediate non-occurrence of food as a predictive failure? Why does not the mismatch between the expectation of food and the percept of no-food trigger premature reset of attention, extinction, and exploratory behavior? The model suggests how a “spectral timing” circuit $S \rightarrow T$ operates in parallel with the fast $S \rightarrow D$ emotional conditioning circuit. Learned timing within $S \rightarrow T$ prolongs the inhibition of the orienting subsystem, and thereby enables attention to be maintained on salient goal-related cues within the expected 6 second delay. If food does not occur thereafter, the adaptive timing circuit becomes quiet. Subsequent mismatches do trigger attentional reset, extinction, and exploration. Grossberg and Merrill (1992) predicted that a spectral timing circuit occurs in the dentate-CA3 circuit in order to explain many conditioning data from the labs of T. Berger and R. Thompson; e.g., Berger *et al.* (1986). Nowak and Berger (1992) have since reported evidence consistent with the spatially organized spectral representation that we predicted to occur at dentate cells.

If hippocampus is removed, then animals and humans have problems with DNMS and related tasks that involve stimulus delays. In the model, a similar thing happens when the T circuit is removed. In addition, as Eichenbaum *et al.* note, “both DNMS performance at brief delays and single-pair object discrimination learning with brief intertrial intervals” are spared in hippocampal subjects. In the model, this is true because the fast $S \rightarrow D \rightarrow S$ attentional circuit remains intact. Long interstimulus delays, say of a day, also spare the performance of animals in some conditions (Mishkin *et al.*, 1984). These results led Eichenbaum *et al.* to claim that “the hippocampal system subserves a memory store of *intermediate* duration”. These results can be explained by the model without positing any

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such “memory store”. At short delays, the fast feedback $S \rightarrow D \rightarrow S$ system helps to focus attention. The failure of blocking at intermediate delays due to the removal of T in the $S \rightarrow T$ circuit causes little problem at long delays because potentially competing cues, being so widely separated in time, decay before they can compete.

Why the hippocampal formation should play a role in spatial orientation is also clarified within this modelling framework when one goes on to consider how an animal can orient its goal-directed behaviors with respect to sets of environmental landmarks that vary in their motivational salience. Many groups are now actively working to model this spatial orientation competence. Some properties that need to obtain in a successful model are summarized in Grossberg (1987).

Taken together, these modelling results clarify the neural mechanisms that may subserve many of the data that Eichenbaum *et al.* review, and caution against arguing that modulation of a behavioral process by a brain region implies that the brain region internally represents the information that is modulated.

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