Continuing Commentary

must be bound into the trace along with other aspects of the experience, such as its content and context. The postulate that the hippocampal component accepts only consciously apprehended information as its input, and so can only bind that type of information, helps explain why the hippocampus is important for forming relational, but not simple, associations. Consciously apprehended information is, by its nature, relational (Baars 1988). To be conscious of something is to be able to comment on it, which involves (at a minimum) an ability to place the object of one’s attention in relation to some other object or event—that is what a comment is. Once in consciousness, the information is no longer isolated in a domain-specific module but is immediately accessible to other systems that store knowledge and can place one event or stimulus in relation to another.

This also helps explain the flexibility noted by Eichenbaum et al. It does not depend only on the relational representation of the memory trace but also on the fact that the memory trace is available to consciousness. Like all things in consciousness, it can be inspected; its individual elements can be noted, manipulated, and controlled. The perihippocampal structures Eichenbaum et al. associate with intermediate term memory may be involved in holding and manipulating information in consciousness for that brief period of time that is necessary for the relevant associations to be formed (see Moscovitch & Umiltà, 1990, 1991, for a discussion of the relation between consciousness, working memory, and conscious recollection).

The idea that the hippocampal component obligatorily picks up all information that is consciously apprehended may provide a link with O’Keefe and Nadel’s (1978) hypothesis that the hippocampus is the substrate for spatial memory. If space is a medium in which all events occur, space provides the context for all our conscious experiences and is bound as an attribute in all memory traces. To speculate further, it may be that structures involved in processing spatial information provided the primordial substrate for consciousness. Space is relational by its nature and provides a natural domain in which information from various modules can be integrated to form relational representations.

Does this theory of recovered consciousness also apply to mammals (and perhaps other organisms) that are not human?

The type of consciousness to which I refer is primitive. It is not equated with self-awareness (Gallup 1985; Stuss 1991) but merely with awareness of stimuli or events. This type of primitive consciousness should be in the realm of capabilities of other mammals. How are we to know if it is? Consider the case of blindsight. Initially, it was the behavior of monkeys with occipital lesions that prompted investigators to reconsider the possibility that humans who claim to be blind can process visual information without awareness (for review, see Weiskrantz 1986). Having established that humans with occipital lesions, like their simian counterparts, can respond to visual stimuli in the blind field, the interesting question now concerns monkeys: If tests of vision require conscious awareness rather than mere response to a visual stimulus, will monkeys, like humans, behave as if they are blind? A recent experiment by Cowey and Stoerig (1992; 1994) suggests that the answer is “yes.” Monkeys are trained, in the intact field, to distinguish between the presence and absence of a stimulus. On trials when the stimulus is presented in the scotomata field, monkeys treat that stimulus as if it were absent. That is, they display the syndrome of blindsight in both of its manifestations—preserved sight on tests that do not require awareness and impaired sight on tests that do. If it is true of monkeys, I predict that investigators will soon show it to be true of other mammals.

If Cowey and Stoerig’s experiment does show that some animals, like humans, are aware of their experiences, then my theory of recovered consciousness can apply to them as well. The hippocampal component in animals, as in humans, only accepts input that was consciously apprehended and binds into a memory trace those neural components that gave rise to the conscious experience.

I do not mean to imply by my speculations that the nature of human consciousness is comparable to that of other mammals in all respects (see Tulving & Markowitch’s (1994). No doubt there are important differences; for example, awareness of self may be peculiar to us and some of the great apes (see Gallup 1985; Stuss 1991). Moreover, the cognitive capacities and unusual of different species are likely to color their consciousness. By implication, the memories they acquire and recover. But the basic stuff of consciousness that allows one to be aware of one’s perceptions and thoughts, and that pervades one’s memories, may be common to many mammals and perhaps other organisms, such as birds, in whom the hippocampus also plays a prominent role in memory. Studies such as Cowey and Stoerig’s and Gallup’s lend substance to these assertions.

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Sequential processing of “items” and “relations”

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Abstract: Eichenbaum et al. (1994a) hypothesized that perceptually distinct items and the relations among them are processed sequentially by the parahippocampal region and the hippocampal formation, respectively. Predictions based solely on their models’ sequential processing feature might prove easier to disconfirm than those based on its representational features. Two such predictions are discussed. (1) Double dissociations should be impossible following hippocampal vs. parahippocampal lesions, and (2) hippocampal lesions should not exacerbate impairments that follow complete parahippocampal lesions.

A great deal of evidence suggests that the hippocampal formation has an intermediate-term memory function and a special role in relational-information processing. As Eichenbaum et al. (1994a) point out, their model is not the first to embrace these two apparent properties of hippocampus-dependent memory, but unlike models that attribute the temporal properties to the representational ones, Eichenbaum et al. suggests that they are determined separately and sequentially by different components of a “hippocampal system.” The idea that the temporal properties of hippocampus-dependent memory are ancillary to its representational properties is more parsimonious than Eichenbaum et al.’s view, in which these properties are determined separately. Therefore, the onus is on Eichenbaum et al. to convince us that the former, simpler assumption should be abandoned.

Eichenbaum et al. do a nice job of demonstrating that their model outperforms others in accounting for extant findings that pertain to the temporal and representational properties of hippocampus-dependent memory. It is through this type of scorekeeping that their ideas concerning intermediate-term and relational-information processing win support. Not surprisingly, many of the initial commentaries on the model question this characterization of the mnemonic functions of the hippocampal formation and parahippocampal region, and through the same kind of scorekeeping, points are taken away from the Eichenbaum et al. team each time an experimental result is noted that doesn’t fit the representational features of their model.

It is difficult to know a priori the extent to which any memory task requires relational processing, and this problem was acknowledged by several of the original commentators and by Eichenbaum et al. This difficulty guarantees that debate about the representational properties of hippocampus-dependent memory will continue for a long time. Meanwhile, an alternative strategy
for evaluating Eichenbaum et al.'s model could rely on certain predictions that are potentially easier to disconfirm. Such predictions stem from one of the nonrepresentational features of the model—the idea that individual items and the relations amongst them are processed sequentially within the parahippocampal region and the hippocampal formation, respectively. This sequential-processing feature implies a one-way interdependence between these two regions; the hippocampal formation can only process relational information about items represented in the parahippocampal circuitry (p. 453). This one-way interdependence requires at least two predictions that are not explicitly addressed in the target article: (1) double dissociations on any two memory tasks will be impossible to demonstrate in subjects with hippocampal versus parahippocampal lesions; (2) hippocampal lesion should not exacerbate the memory impairment produced by a complete lesion of the parahippocampal region. The value of these predictions is that neither requires assumptions about the representational properties of the hippocampal formation of parahippocampal region.

The prediction about the impossibility of double dissociations was eluded to briefly by Aggleton in his commentary (p. 472). In fact, findings have been reported that appear to be at odds with this prediction. Hippocampal lesions produced only a mild impairment in water-maze performance (Morris et al. 1982; Sutherland et al. 1983), but perirhinal cortex lesions produced only a mild impairment or none at all (Wig & Bilkey 1994a, 1994b). The reverse was found with object-based delayed nonmatching-to-sample: Perirhinal cortex lesions produced severe deficits (Meunier et al. 1993; Mumbly & Pinel 1994), but hippocampal lesions produced either mild deficits or no deficit at all (Mumbly et al. 1992; O'Boyle et al. 1993; Rothbllat & Kromer 1991). The foregoing analysis should be viewed with caution because each study examined only one of the two tasks and only one of the two lesions; the lesions might have differed in important ways across these experiments. It is more helpful to look for dissociations within single experiments that assess the same hippocampal and perirhinal subjects on multiple tasks. The important point is that any two tasks that revealed a double dissociation with hippocampal and parahippocampal lesions would disconfirm the sequential-processing feature of Eichenbaum et al.'s model. Eichenbaum et al. (1994c) respond to Aggleton's (1994) suggestion that we look for evidence of double dissociations by pointing out that partial lesions of the parahippocampal region that spared corticohippocampal connections would not be expected to eliminate hippocampal processing (p. 504). But, based on their own rationale for combining the hippocampus proper, dentate gyrus, subiculum, and fornix into a functional unit—the most restricted lesion that produces a maximal deficit on any task must include all of these structures—they should agree that lesion completeness, in this case the degree of corticohippocampal disconnection, should be reflected in the severity of a functional deficit. Any corticohippocampal disconnection that was substantial, even if incomplete, should have some functional consequence, even if not maximal.

It is important to note how the second prediction—that adding a hippocampal lesion will not exacerbate the memory impairment produced by a complete parahippocampal lesion—differs from the prediction outlined in the commentary by Squire et al. (1994). Those commentators point out that, if Eichenbaum et al.'s model is correct, performance on tasks that require relational processing should be no worse after conjoint hippocampal and parahippocampal lesions than after lesions restricted to the hippocampal formation (p. 496). The model does make that prediction, but findings that bear on it are also open to debate because the prediction is specific to assumptions in the model about the representational properties of hippocampal processing; it therefore requires that we know how subjects solve the problems. On the other hand, any task performance deficit that was exacerbated by adding even a small hippocampal lesion to a complete parahippocampal lesion would be problematic for the sequential-processing feature of Eichenbaum et al.'s model. So would any memory deficit that could only be observed following the combined lesion. To the best of my knowledge, the relevant findings have not yet been reported. Of course, without the use of appropriate tasks, these strategies will tell us nothing about whether the hippocampal formation is specialized for processing relational information or whether individual items are represented within parahippocampal circuitry for intermediate-term intervals. But they could potentially inform us in an instant that the sequential-processing feature of the model is not tenable.

Even without empirical evidence to address these predictions, there is reason to be skeptical of the one-way interdependence implied by Eichenbaum et al.'s model. It is difficult to imagine how perceptually distinct items could, in a strict sense, be represented only at an earlier stage of processing than relational information about those items. It is intuitive that experiencing the relations among perceptual items helps determine exactly what will be later perceived and treated as an individual item. There accordingly seems to be a need for two-way interplay between modules that process information about items and their relations. To be fair, Eichenbaum et al. do propose that relational processing by the hippocampal formation serves to modify long-term neocortical representations, but just how it serves to modify the individual representations in the parahippocampal region is not outlined in their model. Rather than focusing only on the parahippocampal-to-hippocampal formation connections, a more complete model would ascribe a role to the reciprocal connections as well. Eichenbaum et al.'s argument that even single isolated findings should not be ignored would then be applied in an anatomical sense to the projections from the hippocampal formation to the parahippocampal region, which are largely ignored in their model. Perhaps these reciprocal connections allow hippocampal processing to affect "tuning" or biasing of items within separate processing modules (p. 458) in the parahippocampal region. The result might be a model consistent with Eichenbaum et al.'s, only less constrained.

The hippocampus seen in the context of declarative and procedural control

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Abstract: Various apparently incompatible theories of hippocampal function have been proposed but integration is now needed. It is argued that the involvement of the hippocampus is most clearly seen when the animal needs to extrapolate beyond current sensory information. Such control can involve both the initiation of behaviour in the absence of appropriate sensory input and the inhibition of behaviour that might otherwise be triggered by current sensory input.

The hippocampus occupies a place of special distinction in the brain. Not only does it have its own journal, but five major reviews of its function have now appeared in Behavioral and Brain Sciences (O'Keefe & Nadel 1979; Olton 1979; Gray 1982; Rawlins 1985; Eichenbaum et al. 1994a). Each proposes a different function for this region and explains some of the data but leaves others unexplained. The reader could be forgiven for being somewhat confused. Are these rival accounts or can they be reconciled? The latest, by Eichenbaum et al. offers hope of synthesis, which I believe can be obtained by integrating the ideas of Hirsh (1974) and looking more closely at the role of the hippocampus in the production of behaviour.

I disagree with Eichenbaum et al. that the hippocampus is involved primarily in the organization of declarative rather than procedural memory. Declarative memory will usually involve relations between events, but in my terms will always be "off-line" (Hirsh 1974) relative to more direct links between sensory input and behaviour. In many learning situations, parallel declarative and