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Remembrance of futures past

Kathryn J. Jeffery

Department of Psychology, University College London, 26 Bedford Way, London, WC1H OAP, UK

Much behavioural and physiological evidence suggests that the hippocampus encodes space. Puzzlingly, however, hippocampal damage also disrupts episodic memory. A recent study shows how these two faculties might be related, finding that the spatial firing of hippocampal 'place cells' is sometimes modulated by what the animal has recently done or what it will do next. Thus, the cells encode something resembling a context, or episode, collectively forming a potential substrate for episodic memory.

Episodic memory (memory for life events) is peculiarly sensitive to hippocampal damage, suggesting a mnemonic role for the hippocampus. However, recordings of hippocampal neurons in rodents (and, more recently, humans [1]) find that the cells are most strikingly responsive to the location of the animal, leading to the influential hypothesis that the hippocampus encodes a 'cognitive map', for use in navigating [2]. Reconciling the mnemonic and spatial views of hippocampal function has been difficult, because the spatial responsiveness of the cells ('place cells') is so conspicuous, and evidence for other kinds of encoding has been conflicting (for discussion, see [3]). Now, evidence has been found that place cells can encode not only current spatial location, but also where the animal has just been and where it is going next [4]. This simultaneous encoding of places past, present and future might allow the brain to store a temporally ordered representation of events.

Modulation of place cells by internal factors

The spatial specificity of place cell firing has long been the most intensively-studied property of these cells, and much evidence shows that sensory cues are important in localising their preferred firing locations (known as 'place fields'). However, recent findings indicate that there is also a modulation of place fields by factors internal to the rat, such as its intentions or expectations. Such findings have added to the growing body of evidence suggesting that the cells might have a broader role than the encoding of place *per se*. In particular, two recent studies, by Wood *et al.* [5] and Frank *et al.* [6], found that place cells recorded in a spatial alternation task fired differently, even if the rat was in the same place, depending on where the rat was in its sequence of actions (see Box 1). Because these tasks were alternating tasks, however, it was not possible to determine unambiguously whether the cells were responding to what the rat had just done ('retrospective coding') or what it was about to do next ('prospective coding'). They might also have been responding to movement cues ('path integration') telling the cells how far the rat had travelled since last encountering a particular sensory cue. Ferbinteanu and Shapiro [4] have now disentangled these various factors and confirmed that place cells do indeed show both retrospective and prospective coding, that both kinds of modulation coexist within a given journey and that modulation occurs independently of path integration.

Ferbinteanu and Shapiro devised a non-alternating task that dissociated where the rat was going from where it had come from, and in which any path integration distance signal would necessarily vary independently of other factors. Rats performed a spatial memory task on a 'plus' maze (Figure 1a), in which the goal arm of the maze was switched periodically from east to west, and the start was varied pseudorandomly between north and south arms. Thus, the rats could make one of four kinds of

Corresponding author: Kathryn J. Jeffery (k.jeffery@ucl.ac.uk).

Box 1

The modulation of place cells by factors internal to the rat, as well as just by 'place', was recently explored in two related studies by Frank *et al.* [6] and Wood *et al.* [5]. Frank *et al.* recorded cells from both hippocampus and entorhinal cortex as rats ran back and forth on a W-shaped maze, and found that some cells exhibited preferred firing locations (place fields) on the central arm that were modulated not just by current location but also by where the rat had come from or where it was going to. For example, a cell might fire when the rat ran up the central arm having just come from the left-hand arm, but not the right, and another cell might fire as the rat ran down the arm if it were to turn left at the end, but not if it were to turn right. Assuming that the cells were modulated by the event closest in time to the actual firing, Frank *et al.* labelled the former pattern 'retrospective coding' (modulation by a previous event) and the latter pattern 'prospective coding' (modulation by a future event). Wood *et al.* published a very similar study soon afterwards [5], recording place cells as rats ran up the stem of a T-maze and returned via alternating left- and right-hand routes. Again, they found cells that fired differently on the stem depending on whether the rat was on a left-hand trajectory or a right-hand one.

These studies were important because they showed that place cells are modulated by more than just immediate sensory cues. In alternation tasks, however, events in the past are correlated with events in the future, and so prospective and retrospective coding are hard to disentangle. The findings could also have been explained by reference to an internal factor known already to influence place cells – path integration. Path integration is the capacity of animals to track their movements using motion-associated cues such as vestibular and motor signals, and is known both to influence place cells and to be 'reset' by a salient external stimulus [10]. Theoretically, the path integrator could be reset at the start of each journey and then monitor distance traversed, so that the final signal (sensory cues plus distance travelled) would enable a place cell to distinguish a left-hand run from a right-hand one. The design of Ferbinteanu and Shapiro's study enabled a dissociation of these factors.

journey, starting from either of the two start arms and running to one of the two goals, and each journey was largely independent of previous journeys. Disruption of hippocampal afferents with lesions to the fornix impaired performance, confirming that the task did require hippocampal processing.

Recording of hippocampal cells during performance of this task found that many were not only place- but also journey-sensitive, firing differently in a given arm depending on what journey was being executed. Some place fields on the start arm were modulated (switched 'on' or 'off') by which arm was the goal (prospective coding; Figure 1b), and some on the goal arm were modulated by which had been the start arm (retrospective coding; Figure 1c). Encoding was generally unaffected by detours, ruling out motor factors such as body turns or path integration. Interestingly, in trials where the rat made a mistake, both prospective and retrospective encoding were diminished, suggesting a relationship (possibly although not necessarily a causal one) between encoding and navigational accuracy.

In Ferbinteanu and Shapiro's experiment, then, both prospective and retrospective coding were unambiguously demonstrated, and furthermore, both occurred on the same journey, together with journey-independent firing (the more classical kind of place field). It seems that several aspects of the task were being simultaneously encoded by the cells, with different cells monitoring different components (i.e. a population coding). These

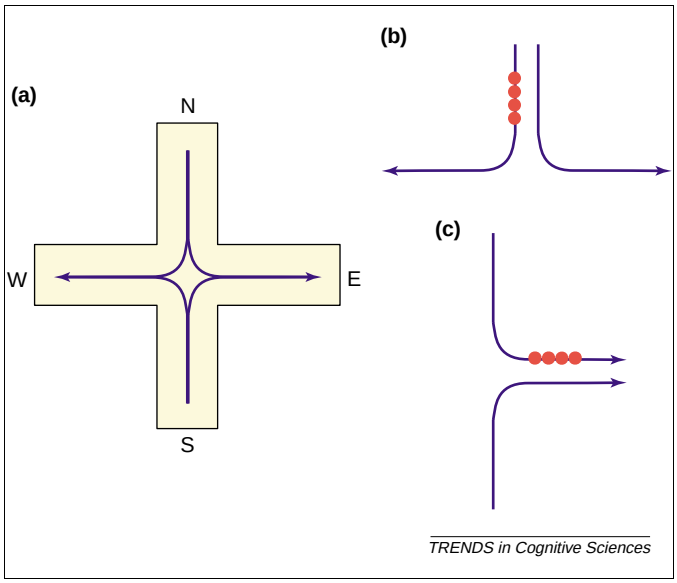

Figure 1. Illustration of prospective and retrospective encoding in the Ferbinteanu and Shapiro task [4]. **(a)** Rats had to run from either of two start locations (the north (N) or south (S) arms) to one of two possible goals (the east (E) or west (W) arms). **(b)** Schematic illustration of prospective encoding by a place cell that fired action potentials (red circles) on the north arm when the rat was on a run that would take it from N to W but not E. **(c)** Schematic illustration of retrospective encoding, in which a place cell fired action potentials on the E arm if the rat had just come from N but not S. (In (b) and (c) the trajectories have been separated so that the journey-specific firing, which occurs on the common part of the run, can be illustrated.)

findings demonstrate clearly that the so-called 'place cells' respond not just to instantaneous place, but to places past and places yet to come – and furthermore, that different time points are encoded within the same ensemble.

What do these findings imply for the encoding of episodic memory? The implications are still far from clear, but this study, together with its precursors, supports two important possibilities: (1) that the simultaneous prospective and retrospective modulation allows for some kind of temporal sequence encoding, for use in laying out the order of events in an 'episode', or that (2) it allows for a context-modulated spatial representation.

Episodic memory or spatial context?

The idea that time is a crucial component of episodic memory dates back to the original formulation of the term by Tulving, who suggested that 'episodic memory receives and stores information about temporally dated episodes or events, and temporal-spatial relations among these events.' ([7], p. 385). If the hippocampus is the substrate for episodic memory we thus ought to find evidence of encoding of time in its neurons. The finding that place cells are modulated by places in the past and the future, as well as the present, supports this notion, providing a possible substrate for the sequencing of events.

Results so far, however, only support a temporal modulation interpretation for the spatial domain (past and future places). Thus, an alternative, albeit related, interpretation of prospective and retrospective encoding is that it amounts to contextual modulation of the spatial signal, where the start and/or goal of a journey comprise the context. 'Context' refers to the encoding, not just of space, but of non-spatial aspects of the environment that collectively characterize a situation [8]. Place cells are

known to respond to contextual stimuli, although the kinds of stimuli that act in this role have not been well established. Those that have been identified so far seem to define a spatiotemporal backdrop against which events can be set. The modulation of place cells by more than simply 'place' extends even to humans, in which hippocampal cells have also been found to be responsive to factors such as the subject's goal, or view, as well as current location [1]. The present studies suggest that the journey that a rat is currently making can define a context too, and can be used to allow association of a particular journey with contextually related events.

The distinguishing factor between the above two possibilities will be whether time turns out to play a special role in place cell encoding, or whether it is just another context cue. In fact, modulation of place fields by the rat's journey might be more complex than it appears at first, because another study, using a broadly similar alternating task on a Y-maze, has failed to find such 'trajectory encoding' [9]. This puzzling discrepancy suggests a sensitivity of the phenomenon to as-yet-unidentified factors which might turn out to provide important constraints on how we conceptualize the information encoded by place cells.

The future…

What next? It would be interesting to know, first, whether prospective and retrospective coding can co-occur not only in the same journey, but at the same moment in time. One way of doing this would be to see how place cells fire on a double-alternation version of the Wood *et al.* task (left–left–right–right) so that, for example, an about-to-turn-right run might also be distinguished by where the rat has just come from. It would also be interesting to find out how many steps in a behavioural sequence the cells can encode before the discrimination breaks down; in other words, how fine-grained is the sequencing? Does the granularity correlate with the ability of rats to remember behavioural sequences? And finally, we need to know whether the 'space' and the 'time' influences on these cells can be dissociated. In other words, is temporally modulated place encoding an example of a broader capacity of the hippocampus to encode sequences of events, or is space in some way fundamental to the activity of 'place' cells – and, by extension, to the encoding of episodic memory?

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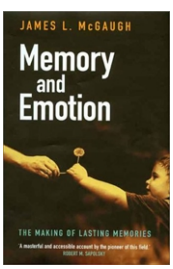
Book Reviews

Strong memories are made of this

Memory and Emotion: The Making of Lasting Memories, by James L. McGaugh (2003) (192 pp.) Weidenfeld & Nicolson, £16.99 ISBN 0 29764 593 5, Columbia University Press, $24.50 ISBN 0 23112 022 2

Elizabeth F. Loftus[1] and Daniel Bernstein[2]

[1]University of California Irvine, Irvine, CA 92697-7085, USA
[2]Department of Psychology, University of Washington, Seattle, WA 98195-1525, USA



'All memories are not created equal.' So writes James McGaugh in his charming and lucid book *Memory and Emotion*. It is more than deserving of the praise lavished upon it by Stanford neurobiologist, Robert Sapolsky, who has called the book 'A masterful and accessible account by the pioneer of this field'. What the book is really about is how experiences activate hormone and brain processes that serve to create strong memories. Strong memories can be created by repetition, but they can also be created when emotional arousal is part of the experience. Once made strong, they can be lasting and relatively immune to distortion. Relatively immune, perhaps, but we would stress that even lasting memories are prone to distortion – a point we will return to later.

McGaugh's field – the neurobiology of learning and memory – has a fairly recent history, much of which he recounts in the early chapters of the book. It is a history that is far shorter than that of other sciences such as biology, chemistry, physics and astronomy. It is also a history a fair bit of which McGaugh personally lived through, and thus his readers are treated to a story that comes alive through his eyes of contemporaneous experience. McGaugh's journey to becoming that pioneer and now one of the world's most pre-eminent neuroscientists began in earnest when he entered graduate school in Psychology at Berkeley in 1953. He didn't just *read about*

Corresponding author: Elizabeth F. Loftus (eloftus@uci.edu).