Interference during rapid episodic encoding and its reduction by recruiting spiking neurons

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1 The problem of interference

In all the points made below, which generally make a number of important statements about the significance of a set of events, it would be useful to present clear example simulation results.

1.1 Interference during the acquisition of novel autoassociative representations

We presuppose that autoassociative representations established through strengthened recurrent fiber synapses in a region such as dentate gyrus (DG) do not exist *a-priori* for novel items. Encoding such a representation for novel input may therefore require a number of repetitions of the same patterns of simultaneous input spikes, so that spike timing dependent plasticity can sufficiently potentiate recurrent synapses between spiking neurons in the target region and between the source of the novel pattern of input spikes and such target neurons. When it is easily possible to effect another occurrence of the novel input, repetition can be accomplished in that way. Presentations of the input may then occur at different intervals and within different sequences of input patterns, producing an "interleaved" data protocol that enables autoassociative encoding of each item even if the spike patterns representing different items overlap.

Encoding of a novel autoassociative item may be possible even when occurrences of the input cannot be effected. In this case, the necessary repetition of spiking activity may be accomplished through the use of a synapse independent short-term buffer that maintains patterns of spiking. A mechanism for such a buffer that is supported by the physiology and observed responses of pyramidal neurons in layer II of entorhinal cortex has been presented in prior work (Lisman and Idiart, 1995; Koene, 2005).

1.2 Consequences of input that elicits overlapping patterns of spikes in a synapse independent short-term buffer

A short-term buffer with persistent firing properties that do not depend on synaptic connectivity relies on intrinsic properties of the spiking neurons, such as an after-depolarization (Klink and Alonso, 1997). The spiking neurons also experience fast after-hyperpolarization (AHP) after each spike. It is therefore not possible to maintain successive patterns that share spiking neurons in such a buffer without auto-completion of spike patterns due to input either from strengthed recurrent fibers within the buffer[1]or from a region with recurrent fiber synapses that already encode a corresponding representation[2]. In the case of novel items, the AHP of the spiking neurons forces the maintained spiking representations to become non-overlapping (a sparse encoding).

A similar process of separation necessarily occurs during novel autoassociative encoding with STDP if random activity in a target region such as DG, with initially weak excitatory recurrent fiber synapses, is used to encode an input map for spikes maintained in a buffer. Postsynaptic spikes in the autoassociative network are followed by AHP, so that different postsynaptic spikes occur within the effective time interval for STDP at synapses responding to presynaptic activity elicited by succesive buffered spike patterns. A subset of neurons in the autoassociative network that repeatedly spike in synchrony with a specific pattern of input spikes can establish significant

[1]Some recurrent fibers exist in layer II of entorhinal cortex, a region that may be the location of a short-term buffer based on persistent firing.

[2]A circuit of reciprocal pathways may exist between a buffer region such as ECII and potential regions of autoassociative encoding such as ECIII or DG.

excitatory recurrent synaptic strengths. For each of the buffered novel input patterns, a distinct autoassociative representation is synaptically encoded in this scenario. Overlapping sets of neurons may come to represent novel items in an autoassociative region such as DG, despite the separation of those items in the buffer, if a previous input map of sufficient synaptic strength already exists, so that input from more than one item maintained in the buffer shares one or more of the same target neurons.

1.3 Interference during episodic retrieval and encoding due to overlapping autoassociative representations

Overlap between the sets of neurons that represent different items in autoassociative memory may more commonly occur as the result of possible interleaved learning, as noted above. If two items occur in a sequence and the representations of the two items overlap to such a degree that the activity of the non-overlapping set of neurons in the second representation is not sufficient to enable autocompletion of the whole spike pattern then the interference caused by the spiking and subsequent AHP at neurons of the first pattern inhibits a possible error correcting role of autoassociative retrieval during episodic retrieval (Lisman, 1999). Instead, pattern errors during episodic retrieval may persist or even worsen and exacerbate as each autoassociative representation is used as part of a retrieval cue for subsequent items in a sequence.

During episodic encoding, the reliability of resulting heteroassociative representations may be weakened by interference due to overlap in the sets of neurons that spike for different autoassociative items that appear in a sequence: A novel episode may occur only once. A corresponding sequence of item representations may be maintained in the ECII short-term buffer[3]. Episodic learning has no interleaved learning protocol. In the case of non-overlapping item representations, STDP at recurrent fiber synapses in CA3 (with slow NMDA channels) can establish graded synaptic strengths that reflect the ordinal interval between items in a sequence (Jensen and Lisman, 1996; Koene and Hasselmo, 2005). An episodic cue is thereby encoded for each successive item in the sequence. In the case of overlapping item representations, if autocompletion succeeds in autoassociative memory then the consequent input to CA3 during episodic encoding may confuse the intended grading of synaptic strengths, since some input occurs for multiple items and therefore much more often. If autocompletion in autoassociative memory fails due to a large overlap then the consequent input to CA3 may be unable to elicit spiking in the worst case. Otherwise, the combination of contextual input from ECIII to CA3 and input from DG to CA3 via strong mossy fibers may still elicit corresponding spikes in CA3 according to a previously learned input map between DG and CA3. The input from autoassociative memory would already be separated into item representations with reduced overlap. If the resulting size of the set of spiking neurons in CA3 that represent individual items within a sequence is very small then the encoded episodic memory may be unreliable. When episodic encoding must take place by maintaining a sequence of spikes after a single presentation then the optimal input to the heteroassociative network in CA3 is input with minimized overlap, i.e. input activity produced by item representations that have already been largely separated (sparsely encoded) in autoassociative memory.

2 Reducing the degree of interference by recruiting spiking neurons

The problem of interference due to the overlap between known autoassociative representations may be reduced without risking a significant loss of representative power when encoding episodes after a single presentation if we presuppose that the levels of activity in an autoassociative network such as DG imply that many neurons coincidentally spike at around the same time as the spiking of neurons involved in the activation of an autoassociative representation. Some of these “coincidental coactivators” may have weak but extant synaptic connections with the input and with the neurons in the autoassociative representation. Through STDP, a subset of the coincidental coactivators that is active in temporal proximity with the spiking representation of an autoassociative item once in each of a number of theta cycles may be recruited into the representation. Such recruitment reduces the proportion of an autoassociative item representation that overlaps with another representation in the sequence being encoded, thereby improving the expectation that autocompletion is acheived for a correct and significant input cue to episodic memory in a region such as CA3.

The separation of autoassociative representations that initially shared a significant proportion of spiking neurons is a mechanism of multiple instantiation. Such multiple instantiation can enable the learning of episodes that contain more than one instance of a specific autoassociative item. An

[3]Maintenance of an episode in a short-term memory may be aided by autocompletion if recurrent fibers or a reciprocal network are available.

obvious example is the situation when we are told to remember a new telephone number, such as 232-4489, in which the individual numbers are well known and may occur more than once. In general, the ability to multiply instantiate known items may be essential in order to uniquely identify events in an ordinal or temporal context, even when those events appear otherwise identical.

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