Abstract: A method is proposed where static patterns or snapshots of cortical activity that could be stored as hyperassociative indices in hippocampus can subsequently be retrieved and reinjected into the neocortex in order to enable neocortex to then proceed to unfold the corresponding sequence, thus implementing an index-based sequence memory storage and retrieval capability.

A central aspect of the target article is the neocortical junction that is encoded in the hippocampus as an index. Hyperassociative rapid eye movement (REM) dreams could be retained to constitute the hippocampal index. During memory retrieval, elicitation of the appropriate index from the hippocampus by internal or external stimuli enables the subsequent retrieval of cortical content using the index. In the elaboration of this proposal, section 5.1 poses two questions: "How does a non-conscious hyperassociative index trigger conscious veridical episodic (i.e., situated in time and place) output? And how is the conscious output constrained to only the relevant episodic memory?" (para. 1).

Llewellyn then provides a descriptive account of how the hippocampus and neocortex interact to achieve this. However, the functional implementation of such a mechanism is not specified. We can consider an analysis of the functional description of this REM-based hippocampal indexing, and the subsequent memory retrieval, in the concrete context of implemented recurrent network models of cortex that we traditionally have employed in sensorimotor sequence learning (Dominey 1995) and in language processing (Dominey & Ramus 2000; Hinaut & Dominey 2013). In this context, static patterns or snapshots of cortical activity that can be stored as hyperassociative indices in hippocampus can subsequently be retrieved and reinjected into the neocortex to enable neocortex to then unfold the corresponding sequence, thus implementing an index-based sequence memory storage and retrieval capability. This is potentially interesting because it provides a form of validation (if successful) of a mechanism that is provided only as a possible solution in the target article. Such an analysis suggests that the index is not a cortical locus or set of loci, but rather a snapshot of the cortical state at that time which can be used, as stated in the target text, as a cue for retrieval in an auto-associative memory. Before addressing the two questions posed earlier, we can first consider these issues: What is the nature of the neocortical junction, and how can it be used in memory retrieval? This first poses the question of what the nature of a conscious memory is.

Memories will tend to implicate the semantic system, which has been demonstrated to encompass a broadly extended network of distributed cortical areas (Binder & Desai 2011; Binder et al. 2009). In this context, the activation necessary to invoke a memory could involve a fairly massive activation of a large distribution of the neocortex. It has been suggested that the hippocampus integrates distributed cortical activity, fusing this coactivation into a memory trace, and that over time the cortex can become independent of hippocampus, with prefrontal cortex taking over the role of integration for more mature memories (Frankland & Bontempi 2005). This suggests the hippocampus would be able to re-instantiate a prior state of cortical activation. Once this state of activation is instantiated, the cortex would then play out the corresponding memory.

We have modeled cortex as a dynamic system of leaky integrator neurons with local recurrent connections (Dominey 1995; Hinaut & Dominey 2013). Such networks have interesting dynamics. In particular, the internal state follows a trajectory such that if the system is put into a state along an existing trajectory, then the system will tend to follow that trajectory from the given state as a point of departure. Based on this property, the state of activation of cortex could be stored as an index by the hippocampus and then reinjected into the cortex. In such conditions, the cortex would then continue in the appropriate trajectory from that point onward, thus "replaying" the corresponding dynamic memory trace. Importantly, such systems display some robustness to noise, but also a form of degraded behavior: if the injected pattern deviates sufficiently from the intended pattern, then the resulting trajectory will deviate from the intended trajectory. This implies that the pattern of activity that is played into the cortex from the hippocampus should be as accurate and complete as possible.

In other words, if a specific memory is to be recalled, then it should be indexed in the most specific manner possible. This suggests, as indicated by Llewellyn, that hippocampus keeps an index of multiple loci that can be used in episodic memory retrieval. If sufficient loci are activated, then the cortex will enter into a state from which a dynamic trajectory will then unfold.

This trajectory can be considered to correspond to the narrativization of experience into a linear sequence. The question that remains, with respect to junctions, is if a trajectory proceeds through a junction, how can the system ensure that it does not deviate onto a different trajectory that traverses that junction? That is, how is the system constrained to recall only the intended or relevant episodic memory? From the perspective of the dynamic systems and recurrent network models that we manipulate, the more that the pattern of cortical activity – entrained by the hippocampal index – is complete and corresponds to the memory to be recalled, the more that the resulting trajectory of cortical activity will correspond to the unfolding of the corresponding episodic memory.

This comment thus advocates the characterization of the cortex as a dynamic system, with state trajectories that can be "replayed" by putting cortex into a past state via hippocampal inputs. This provides a mechanism that is consistent with Llewellyn's proposal and provides potential responses to the questions: "How does a non-conscious hyperassociative index trigger conscious veridical episodic (i.e., situated in time and place) output? And how is the conscious output constrained to only the relevant episodic memory?"

Mnemonic expertise during wakefulness and sleep

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Abstract: We studied the world's most distinguished experts in the use of mnemonic techniques: the top participants of the World Memory Championships. They neither feel the use of mnemonics to be dreamlike, nor does their REM sleep differ from mnemonic-naive control subjects. Besides these empirical data, also theoretical considerations contradict an isomorphism between features of REM sleep dreaming and mnemonic principles.

Mnemonic techniques have been valued since ancient times but have lost attention dramatically for decades. Llewellyn's target article on a possible role of mnemonic principles (ancient art of memory [AAOM]) acting during rapid eye movement (REM) sleep to aid episodic memory processing is therefore a timely and important endeavor. Here we aim to demonstrate that one promising way to test these ideas is to study users of mnemonic techniques, both novices – that is, naive subjects who have been systematically taught mnemonic strategies – and experts who have trained the use of mnemonics for several years. One group of subjects provides a unique opportunity in this regard: Participants of the annual World Memory Championships regularly demonstrate their mastery in mnemonic techniques by memorizing astonishingly large amounts of information (Maguire et al. 2003). During the last two years, we studied the world's most successful memory athletes, who all credited their performance to deliberate training in mnemonics.

A simple qualitative test of the REM-AAOM hypothesis is the question of whether the application of mnemonics actually feels like dreaming: If REM sleep dreaming implements or is isomorphic to mnemonic principles, the use of mnemonics should feel dreamlike during wakefulness. This should be true in particular for the more experienced users of mnemonics. We asked 34 mnemonic experts (aged 32.1 ± 11.3 years, 12 female) in the top 100 memory-sports-world rankings and 37 mnemonic novices (aged 24.4 ± 4.9 years, 9 female) who participated in an introductory course in mnemonic techniques whether they felt the application of mnemonics to be dreamlike, on scale of 1 (totally dreamlike) to 7 (not dreamlike at all). Neither group felt the application of mnemonics to be very dreamlike, with the mnemonic experts' ratings being even slightly (though nonsignificantly) shifted more to the nondreamlike side of the scale (4.9 ± 1.5 vs. 4.5 ± 1.5, $t = 1.1$, $p > 0.2$).

A test on the neurophysiological level is to compare the REM sleep of mnemonic experts and control subjects naive to mnemonics. If an essential function of REM sleep is to apply mnemonics on recent memory traces, then it should differ depending on how much information was learned before sleep and whether this information was already encoded mnemonically or without the use of mnemonics. We investigated 16 mnemonic experts (aged 27.1 ±9.5 years, 6 female) in the top 50 of the memory-sports-world rankings with polysomnography, both after a day without memory-related activity and after an intense learning session of several hours during which they applied mnemonics on a broad variety of declarative information, and compared them with closely matched controls (aged 27.4 ± 8.5 years, 6 female) without any experience in mnemonic techniques (Dresler et al. 2012).

Despite a huge difference in mnemonic expertise and memory load, we did not find a significant difference in REM sleep duration between the groups (F=1.5, $p > 0.2$) or between the learning conditions (F=0.4, $p > 0.5$) and no interaction effects (F=0.9, $p > 0.3$). Since REM density has been proposed to be implicated in memory processing and to provide a marker of learning potential (Smith et al. 2004), we also analyzed this variable, but also did not find a differences between the groups ($F = 1.0$, $p > 0.3$) or conditions ($F = 0.2$, $p > 0.6$) and no interaction effects ($F = 0.2$, $p > 0.6$). For details, see Tables 1 and 2.

The results of both tests with mnemonic experts do not support the REM-AAOM hypothesis. In our view, this is no surprise, since despite several intuitively convincing similarities between REM sleep dreaming and mnemonic techniques, the two also manifest essential differences. One important aspect of mnemonics, like the method of loci, is to provide a systematic structure that reliably helps to retrieve the complete set of to-be-remembered information. However, REM sleep dreams, with their frequent discontinuities and indeterminacies, do not provide such systematic structure, but rather consist of a chaotic progression of only loosely related elements.

An essential function of mnemonics is to provide easily accessible retrieval cues that help to recollect less accessible information. Mnemonic retrieval cues associated with new information during REM sleep, however, are hard to access after awakening, because of dream amnesia. According to the REM-AAOM hypothesis, somehow they do their job anyway – just on a nonconscious processing level. The mnemonic mechanism seems to be somehow inverted here: During wakefulness, mnemonics provide easily accessible retrieval cues to activate otherwise inaccessible memories, whereas during sleep the REM-AAOM hypothesis presumes them to provide inaccessible retrieval cues that in most cases do not even reach a conscious level when the corresponding memory traces are successfully retrieved. We find this hardly convincing.

Table 1 (Dresler & Konrad). *Time spent in REM sleep, given as mean minutes ± standard deviation*

	Mnemonic experts	Controls
Nonlearning condition	92.1 ± 24.8	93.6 ± 16.4
Learning condition	84.2 ± 22.5	95.4 ± 18.4

Table 2 (Dresler & Konrad). *REM density, given as mean count of rapid eye movements per minute of REM sleep ± standard deviation*

	Mnemonic experts	Controls
Nonlearning condition	4.7 ± 1.2	4.3 ± 1.6
Learning condition	4.5 ± 1.2	4.3 ± 1.2

Another problem of the REM-AAOM hypothesis is its focus on episodic memories: Defining properties of episodic memories already include several mnemonic features like representation in the form of visual images, having a personal perspective, being represented in given order, or being recollectively experienced when accessed (Conway 2009). Even though some of the mnemonic experts that we studied reported that sometimes they would encode also proper episodes mnemonically (e.g., if completeness of details is important), typical applications of mnemonics are discrete or abstract sets of information without episodic structure – for example, telephone numbers or shopping lists. Roughly speaking, mnemonics transform such unrelated bits of information into episodelike structures – for example, imagined stories or mentally travelled routes.

The REM-AAOM hypothesis hence faces a dilemma: Either it proposes that REM sleep mnemonically reprocesses only information that is already episodically structured – in which case the application of mnemonics loses much of its strength – or it widens its focus on declarative memory in general, including also information without proper episodic structure – although for these kinds of stimuli, several studies were unable to find an essential role for REM sleep in memory processing (e.g., Dresler et al. 2011; Genzel et al. 2009; 2012; Rasch et al. 2009).

In conclusion, both empirical data and theoretical considerations contradict the REM-AAOM hypothesis. The world's leading mnemonics users do not feel the application of mnemonics to be dreamlike, and their REM sleep does not differ from mnemonics-naive controls. The REM-AAOM hypothesis focuses on information that normally does not need to be encoded mnemonically, and that is proposed to be encoded mnemonically in a cognitive environment that is not well suited for the application of mnemonics.

Beware of being captured by an analogy: Dreams are like many things

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Abstract: Classic traditions have linked dreams to memory (e.g., "dreaming is another kind of remembering" [Freud 1918/1955]) and