

# Internally-Generated Activity, Non-Episodic Memory, and Emotional Salience in Sleep\*

**James A. Bednar**

Department of Computer Sciences,  
University of Texas at Austin,  
Austin, TX 78712 USA

[jbednar@cs.utexas.edu](mailto:jbednar@cs.utexas.edu)

<http://www.cs.utexas.edu/users/jbednar/>

**Abstract:** (1) Substituting (as Solms does) forebrain for brainstem in the search for a dream “controller” is counterproductive, since a distributed system need have no single controller. (2) Evidence against episodic memory consolidation does not show that REM sleep has no role in other types of memory, contra Vertes & Eastman. (3) A generalization of Revonsuo’s “threat simulation” model in reverse is more plausible and is empirically testable.

## **One dream controller is as bad as another. [Solms]**

The Solms target article persuasively argues that not all dreaming can be uniquely identified with activity in the REM-generating areas of the brainstem (as was proposed in some earlier research). However, substituting the ventromesial forebrain as the single “controller” of dreams, as Solms proposes, seems like a step backwards, even if lesion studies show that the area is important or even crucial for dreaming. As neuroimaging studies make clear, dreaming is a complex process occurring in a system of multiple interacting units distributed across the brain. In such a distributed system, lesion studies cannot provide any means for deciding on a single location as the controller, since in fact there need be no such clearly-defined module. (Thus in Solms’ terms, no single brain area need be able to “activate, generate, sustain and terminate” all dreams.)

A more productive approach might be to focus on the essential aspects of dreaming, and only then to consider how the various brain areas might contribute to this process. The most obvious feature that distinguishes dreaming from waking is that dreaming relies on internally-generated inputs (Bednar and Miikkulainen, 1998), while waking mentation can be traced, at least in part, to data from the senses. There can be many possible sources of this endogenous activity during sleep, all of which could be considered to “cause” dreaming in some sense. Among these, brainstem REM generators do seem to be “a regular and persistent source of cerebral activation during sleep”, as Solms himself acknowledges. Thus there is no mistake at all in focusing on the REM state instead of searching for a single anatomical site to unlock the secret of dreaming.

A second minor point from the Solms article is worth mentioning in passing, since it involves a report most likely published after his article was written. Solms speculates that the cortical backprojections which appear to underlie mental imagery do not project as far back as primary visual cortex, which if true could explain why V1 shows decreased activity during REM sleep. However, backprojections to V1 certainly seem to be present anatomically, and Kosslyn et al. (1999) have shown that mental imagery can in fact be measured in V1, albeit only of a certain kind involving specific locations on the retina. Thus a theory of dreaming would have to explain why the backprojections to V1 do not typically take part in dreaming; it clearly is not because the connections do not exist.

## **Non-episodic memory does *not* require consciousness. [Vertes and Eastman]**

Vertes and Eastman present strong and valid reasons for discarding the idea that explicit episodic memories from the hippocampus are somehow consolidated during REM sleep. However, in several instances they go much further than

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\*From the special issue *Sleep and Dreaming of Behavioral and Brain Sciences* 23(6):908-909.

their cited data would support by concluding that “REM sleep serves no role in the processing or consolidation of memory”. They appear to make this claim because of their unusually restrictive definition of memory, in which “sleep involves basic biological functions and memory requires consciousness.”

Certainly, some types of memory are intricately linked with consciousness, in particular the episodic memory usually proposed for consolidation. However, memory is a very broad term that is applied to an enormous variety of wonderful phenomena, ranging from the strength of the connection between two *Aplysia* neurons (or even the state of charge of a certain capacitor in a computer chip), to vastly more complex processes. Rather than being a specific byproduct of consciousness, memory seems to be quite distributed, localized, and ubiquitous in the nervous system (Gilbert, 1998). Indeed, it is arguably as much of a “basic biological function” as sleep is.

From this larger view, there is currently no reason to conclude that REM sleep serves no role in non-episodic memory processing, despite the lack of clinical impairments from REM deprivation. Given widespread plasticity combined with the strong activity found in many brain areas during REM sleep, the burden of proof is actually in the other direction: unless one can show a plausible mechanism by which the process of learning has somehow been disabled at each local synapse without abolishing activity, one must assume that the activity has the potential to modify those synapses. Plasticity of this sort would presumably underlie non-episodic memories, such as procedural/skill memory (Smith, 1995) and limbic-system emotional associations (Maquet et al., 1996); such effects could be difficult to measure clinically. It is even possible that the episodic and working memory areas quiet during REM sleep might be suppressed precisely so that they would not undergo plasticity while the rest of the brain is processing other types of memory. Such processing could be very important to proposals such as Revonsuo’s (this issue).

### **How solid is the evidence that dreaming is an organized simulation of the world? [Revonsuo]**

Even though I share with Revonsuo a suspicion that dreams are not as random as Hobson and McCarley (1977) proposed, I do not agree that his particular line of argument “shows beyond any reasonable doubt that dreaming is an organized simulation of the perceptual world.” He correctly anticipates most of the argument’s weaknesses, but a few important ones have been overlooked. For instance, he cites differences in narrative richness between dream reports and subjective reports from isolated electric stimulation in temporal cortex. However, these conditions are not comparable, since we know that REM sleep activation is a large-scale phenomenon with at least some spatial and temporal structure. An appropriate experimental control would thus require widespread and ongoing artificial brain stimulation, coupled with temporary deactivation of the same frontal-lobe areas suppressed in REM sleep. If such an experiment were practical, it might demonstrate that dream-like mentation could be generated from random activation; meanwhile we must at least consider it possible.

Similarly, when Revonsuo quotes Foulkes as saying “The simulation of what life is like is so nearly perfect, the real question may be, why shouldn’t we believe this is real?”, Dennett (1991) would probably point out that (1) there need be no “simulation” of life in dreams separate from the experiencing of the dream, and (2) any brain activity contributing to the experience need not be perfect or realistic at all, as long as the processing machinery treats it as realistic. Indeed, as Revonsuo acknowledges, there are many bizarre, non-realistic features of dreams that are obvious only in retrospect.

### **What makes threat simulation so special? [Revonsuo]**

Revonsuo’s general hypothesis for mammals “Dreaming rehearses species-specific survival skills” seems much more defensible than his narrow version for humans: “dream consciousness is essentially a mechanism for simulating threat perception and rehearsing threat avoidance responses and behaviors.” (Unfortunately, the version for humans is the one that is most clearly distinguishable from similar earlier theories, such as Winson, 1990 and Jouvett, 1978.) Threat simulation would seem primarily useful for species which are typically prey rather than predator, and humans clearly serve in both roles. Since Revonsuo acknowledges that “not all dreams are threat simulations”, it seems arbitrary to assume that other commonly-cited dreams (such as flying) are mere side-effects.

Given that threats are not the only situations biologically important to humans, ancestral or otherwise, a much more intuitive hypothesis would be that dreams simulate biologically significant situations in general. In humans “biologically significant” would presumably be approximated as “emotionally salient”, in the absence of some other internal criterion for what is biologically significant. Threats would just turn out to be a particularly well-represented example of such situations, rather than the primary purpose of the system.

In making the case for threat simulation, Revonsuo dismisses most previous proposals for dream function because they do not systematically analyze dream content. Dream content analysis may be very helpful for formulating hy-

potheses, but by itself it cannot offer any definitive criterion for preferring one hypothesis over another because of the enormous and largely unknown biases involved in subjective dream content reports. Even during waking life, we focus disproportionately on emotionally salient events when reporting narratives, as a quick glance at the evening news or the movie listings will attest. Given the particular emotional salience of threatening events (again, witness the bizarre popularity of horror films), finding threatening events overrepresented in reports does not necessarily indicate that they are overrepresented in dreams, and finding them overrepresented in dreams does not necessarily mean that they are specifically generated. At a minimum, to use dream content analysis one must compare dream reports with waking reports as opposed to actual waking life.

Revonsuo also seems to go too far in emphasizing the lack of adaptive function for threat avoidance in modern life. While daily life for many people may be quite dull, certainly those who have served in war, who have lived in the inner city, who have played competitive sports, who have been assaulted, who have encountered a vicious dog, and so on are quite familiar with threatening situations. Despite being relatively safe, people still die every day due to jealous lovers, natural disasters, and many other causes which have been presumably unchanged for millennia. And thus being alert and ready for quick, decisive action in threatening situations is surely not “obsolete”, even if no longer as important as it once was.

### **Revonsuo’s dream model: Why not have emotion precede situation?**

From data showing only a correlation between emotions in dreams and the situations in which they are experienced, Revonsuo assumes a specific direction of causality, i.e. that unpleasant dream situations cause the negative emotions through “threat recognition”. However, common dream features such as emotional continuity in the face of narrative discontinuity (Seligman and Yellen, 1987) would suggest precisely the opposite hypothesis: the brain may somehow activate a certain emotion, which prompts recall of events historically (or perhaps genetically) associated with that emotion.

Reversing the sequence in this way can simplify a key step in Revonsuo’s neural model of dream generation. As originally formulated, his model requires some unspecified mechanism for initially selecting memories by their emotional salience. Such a mechanism is difficult to imagine because it would supposedly operate independently of the current emotional state of the brain, since limbic system areas like the amygdala are activated only later in his process. The model also requires another unspecified (and difficult to imagine) mechanism for deciding “when potentially threatening content is present in visual awareness”, since no feedback for this judgment is available in the model.

Reversing the sequence leads to a simpler and more concrete approach similar to Hobson et al’s AIM model. This model would start with activation of an emotional state in the limbic system along with sparse random activation of the visual system. The initial activation would automatically activate (more or less at random) one or more emotionally-salient episodic memories of waking experience. Such memories would presumably include specific patterns of activity in the sensory association areas and in motor cortex. In the simplest case, the process of activation could simply strengthen the already-present emotional association between the activated units through a simple connection-specific mechanism like Hebbian learning. This model would merely enhance emotionally salient memories at the expense of others, which could be desirable.

Making this model slightly more extravagant to compare with the one proposed by Revonsuo, it could instead generate specific (rather than random) coarsely-determined visual input and/or specific motor cortex activations (Bednar, unpublished research proposal, June 1999). Such a system would amount to supervised training of an association between particular inputs (e.g. threatening situations, as in Revonsuo’s model), particular outputs (e.g. fighting or fleeing), and a given emotional state (e.g. fear). The inputs, outputs, and emotional state would all need to be genetically specified somehow, which is what makes this hypothesis more extravagant than the simpler one above. However, the extravagance is no greater than Revonsuo’s, and this model does not require the presentation of hypothetical scenarios on the input while hoping for the correct response from a brain that has no proposed feedback signal to guide the “threat recognition” process.

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