

Possible Topics

- ▶ Sparse representations, sparse codes, compressive sampling, sparse convolutive nonnegative tensor factorization
- ▶ Optimal codes *vs* attention and attentional modulation
- ▶ Theory of sleep

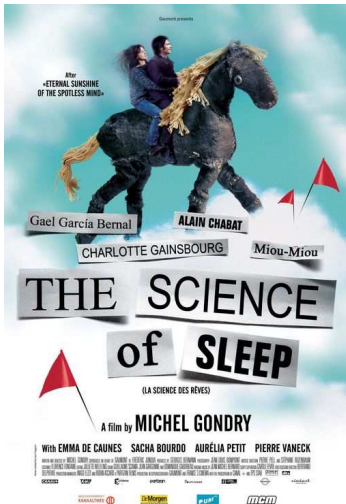
A New Hypothesis for Sleep: Tuning for Criticality

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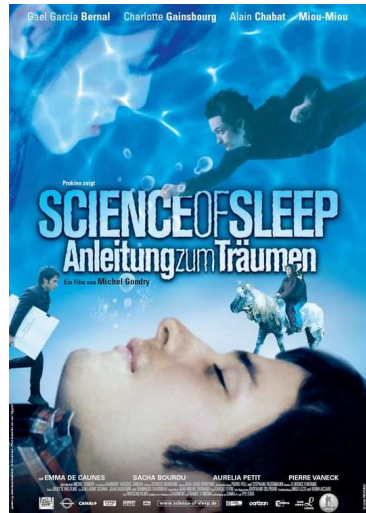
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The Mystery of Sleep



There is enormous interest in sleep, even beyond the scientific community.



Resting versus Sleeping

While it is clear that we rest while we are asleep, it is not at all clear why we need to sleep in order to rest.

It is only on reflection that we realize what a peculiar phenomenon sleep is: most obviously, it is dangerous in that there is a substantial threshold of arousal and a period of befuddlement on awakening.

Unlike hibernation, which has an obvious metabolic explanation, sleep cannot be explained from a purely ecological point of view.

Considering the cost of sleep, sleep must be the only practical way of performing some particular critical function.



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Our purpose here is not to explore “piggy-backed” functions, but to propose a new hypothesis concerning sleep’s core, critical, function.

The Big Mysteries of Sleep

I. Why is sleep necessary?

(Hartmann, 1973)

The Big Mysteries of Sleep

- I. Why is sleep necessary?
- II. Why does lack of sleep cause tiredness?

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The Big Mysteries of Sleep

- I. Why is sleep necessary?
- II. Why does lack of sleep cause tiredness?
- III. Why does tiredness impair cognitive function?

(Hartmann, 1973)

Sleep is for Memory Consolidation I

A troubling lack of evidence

Memory consolidation is the established candidate for the critical function of sleep: the hypothesis is that sleep is an essential part of the process by which long-term memories are formed (Walker, 2005).

For such a popular and widely tested theory (Fishbein and Gutwein, 1977; Gutwein and Fishbein, 1980; Sejnowski, 1995; Sejnowski and Destexhe, 2000), the experimental evidence is surprisingly inconclusive (Allen et al., 1972; Horne and McGrath, 1984; Vertes and Siegel, 2005; Foster and Wilson, 2006).

Sleep is for Memory Consolidation II

A troubling lack of evidence

“Evidence for the influence of sleep discharge patterns on memory traces remains fragmentary.” (Maquet, 2001)

The original hypothesis (Fishbein and Gutwein, 1977; Bloch et al., 1979) has been weakened in response to seemingly contradictory experimental results (Vertes and Eastman, 2000; Finelli and Sejnowski, 2005) to the point that some consider it vacuous (Siegel, 2005).

Sleep, Memory and Cognition

Basic phenomenology:

no sleep \longrightarrow tiredness

tiredness \longrightarrow impaired cognitive function

sleep \longrightarrow $\left\{ \begin{array}{l} \text{(a) slightly scrambles brain} \\ \text{(b) abolishes tiredness} \end{array} \right.$

Tiredness impairs most aspects of cognition: short term memory, attention, retrieval, concentration, learning, planning, insight, multiplexing, etc.

Evidence for Criticality

There is converging evidence, from a variety of sources, that the brain operates at the critical point, i.e., at the edge of chaos.

- ▶ Associative networks (Crick and Mitchison, 1983; Hopfield et al., 1983; Hopfield and Brody, 2001)
- ▶ Avalanche behavior in cortical slice (Beggs and Plenz, 2003, 2004)
- ▶ Balance between excitation and inhibition
- ▶ Impulse response with TMS+EEG (Massimini et al., 2005)

Sleep Allows Brain to be Nearly Critical

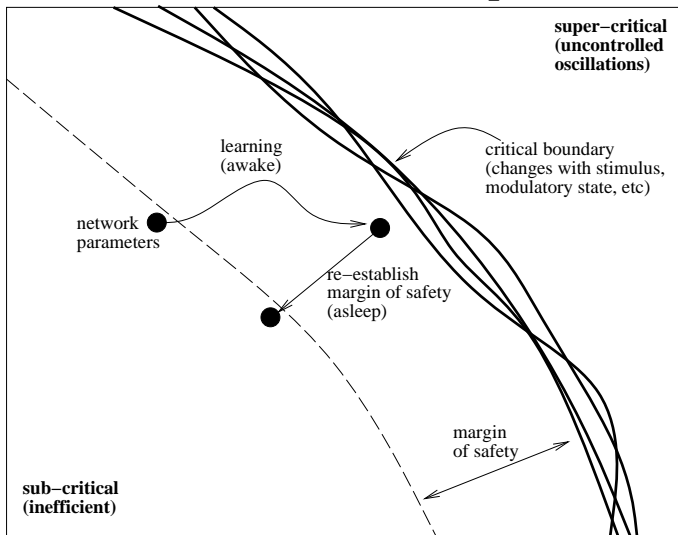
- ▶ More memories, faster retrieval, longer retention of sensory stimuli \Rightarrow stronger synapses.
- ▶ Unchecked, leads to phase transition: supercritical, sudden uncontrolled oscillations.
- ▶ Solution: establish margin of safety (during sleep).
- ▶ Margin consumed during wakefulness.
- ▶ When margin used up: reestablish with sleep.
- ▶ When sleep impractical: buy safety at expense of processing efficiency. (Tiredness.)

Tiredness: An Emergency Mechanism

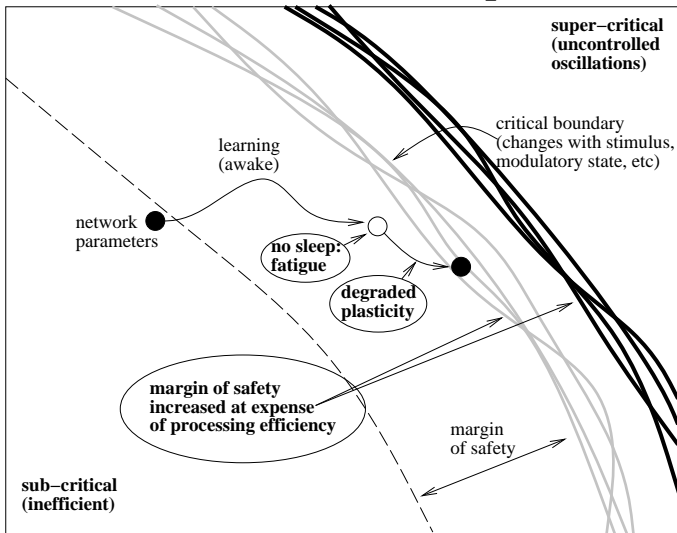
Tiredness explained: an emergency mechanism to diminish the threat of super-critical behavior when sleep is not possible.

If this is true, then it should be risky to suppress tiredness.

Network Parameter Space



Network Parameter Space



Circadian Rhythm

Sleep in adults is typically driven by a circadian rhythm.

The circadian rhythm has an obvious ecological role.

According to the tuning-for-criticality theory, the circadian rhythm also has another purpose.

- ▶ Sleep: mechanism to avoid super-criticality.
- ▶ Tiredness: emergency mechanism to avoid super-criticality.
- ▶ Circadian rhythm: mechanism to avoid tiredness.

Super-criticality: extremely dangerous.

Tiredness: somewhat dangerous.

Clinical Depression

Speculation

Clinical depression is exacerbated by too much sleep and treatments include sleep deprivation (Wirz-Justice and den Hoofdakker, 1999) and modafinil, a drug which suppresses tiredness (Menza et al., 2000).

Perhaps one contributing cause of depression is a tuning-for-criticality mechanism that is too strong, resulting in a system that is overly sub-critical, causing an inability to sustain concentration, a reduced short-term memory capacity, and lethargy. Furthermore, the fact that the depressed brain is sub-critical could reduce the need for sleep below what is regulated for by the circadian rhythm, resulting in insomnia.

Cetaceans

Supporting Evidence

Cetaceans cannot sleep in the normal way: an unconscious cetacean would drown. Many cetaceans sleep with half their brains at a time: one half of the brain remains awake, and one eye remains open (Mukhametov, 1985). (This example alone allows us to discount ecological theories of sleep.) One disadvantage of unihemispherical sleep is that it appears to make REM impossible; at least, it has not been observed in cetaceans (Mukhametov, 1985; Lyamin et al., 2000).

According to the tuning-for-criticality theory of sleep, this requires that the dolphin brain be less subtly tuned for criticality, and therefore less efficient than the brains of terrestrial mammals. Cetaceans in general, and in particular those such as the narwhal and dolphin that hunt and that live in challenging environments, are unusually highly encephalized.

Criticality in Cortical Slice

Supporting Evidence

Evidence for critical behavior is provided by the observation of avalanche-like spiking in cortical slices (Beggs and Plenz, 2003, 2004).

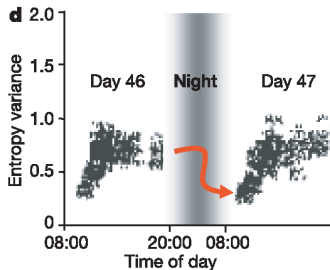
Extended recordings are made of slices using an electrode array. It is observed that spiking is intermittent, with periods of activity interleaved by periods of quiescence. By dividing time into short bins and counting how many electrodes are active in each bin, it is possible to define the length and size of the periods of activity, or avalanches. The number of avalanches of a given duration and the number of a given size both fall according to power laws: $N \propto n^\gamma + C$ where C is a constant, N is the number of events and n the duration or size with scaling exponents $\gamma = -2$ for duration and $\gamma = -3/2$ for size.

Bird Song Learning & Sleep

Derégnaucourt et al. (2005)

Zebra finch song quality monitored during acquisition.

- ▶ Learning rapid after awakening.
- ▶ Learning slows as bird tires.
- ▶ Sleep degrades song performance.
- ▶ Birds with most degradation by sleep ultimately attained best performance.

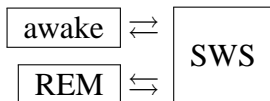


Consistent with tuning-for-criticality hypothesis.

REM, SWS, and Criticality

Phenomena (Aserinsky and Kleitman, 1973):

- ▶ Wakefulness is followed by SWS.
- ▶ REM is followed by SWS.

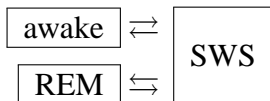


State Transition Diagram

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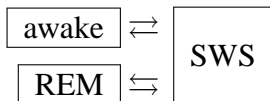
State Transition Diagram

Idea: candidate synapses at risk of involvement in supercritical behavior marked during wakefulness or REM; confirmed and targeted during SWS.

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State Transition Diagram

Idea: candidate synapses at risk of involvement in supercritical behavior marked during wakefulness or REM; confirmed and targeted during SWS.

Implication: REM important for robustness against unexpected conditions, but SWS alone sufficient for most purposes.

Self-Organized Criticality

Our hypothesis regarding the role for sleep is new, but the idea that brain is near-critical, and of “Computation at the edge of chaos,” is not (Turing, 1950; Bak, 1997; Bertschinger and Natschlager, 2004; Chialvo, 2004).

That idea—that the brain’s normal waking plasticity rules organize for criticality—is intriguing, but differs from the hypothesis we advance: that near-critical behavior is the result of tuning during the wake-sleep cycle, and that waking changes, without sleep, would lead to super-critical behavior.

Power-Law Scaling and Criticality

Power-law scaling is typical of critical systems.

Power-law behavior arises in the critical regime of a simple network model (Beggs and Plenz, 2003, 2004; Zapperi et al., 1995).

Does not explain biologically how a neuronal network could develop with the precise synaptic strengths required for this critical behavior.

Growth Model and Criticality

Model of neurite growth (van Ooyen and van Pelt, 1994) shown (Abbott and Rohrkemper, 2006) to give avalanche behavior with correct scaling exponents.

- ▶ Neurons are placed randomly on 2D square.
- ▶ Each neuron is surrounded by imaginary circle.
- ▶ Overlapping circles \Rightarrow connected synaptically, strength proportional to area of overlap.
- ▶ Size of circles changes in response to $[Ca]$.
- ▶ $[Ca]$ integrates spiking behavior.

$[Ca]$ modulates behavior: quiet $\rightarrow \uparrow [Ca] \rightarrow \uparrow$ synaptic strength

Growth/Sleep Model and Criticality

Model identical to that of Abbott and Rohrkempter (2006) except, as suggested by van Ooyen and van Pelt (1994), synapse strength s_{ij} for connection neuron i to neuron j given by $s_{ij} = A_{ij}C_{ij}$ where A_{ij} overlap area and C_{ij} are uniformly drawn from $[0, 2]$. Idea: the A_{ij} are changed during sleep and the C_{ij} during learning.

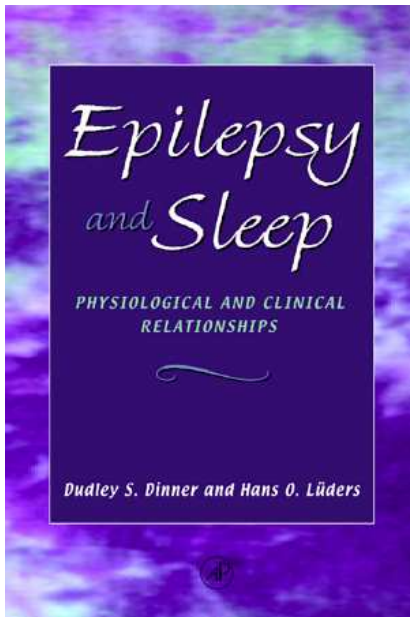
The additional C_{ij} factor did not affect the statistical behavior of the system.

Predictions I

- ▶ Lack of sleep should cause tiredness.
- ▶ Impulse response of cortex during wakefulness near criticality; move closer to the boundary during slow wave sleep (Massimini et al., 2005)
- ▶ Different plasticity regimes should operate during wakefulness, tiredness and slow-wave sleep.
- ▶ MAO inhibitors (which abolish REM) should not cause memory impairment (Vertes and Eastman, 2000; Georgotas et al., 1983).
- ▶ Increased encephalization in species that sleep less (other factors being equal).
- ▶ Sleep time should increase when brain (not body) is growing/shrinking.

Predictions II

- ▶ Down-regulation of synaptic plasticity is another symptom of tiredness; should make learning a new task more difficult during tiredness.
- ▶ Sleep debt accumulated during an extended waking period should be proportional to the fraction of that period during which synaptic changes were permitted; could be evaluated by monitoring the ability to learn during period of sleep deprivation.
- ▶ Combating symptoms of tiredness through constant stimulation or drugs should increase the risk of epilepsy.
- ▶ An increased risk of epilepsy is likely to be a consequence of regular sleep deprivation, particularly among babies and children, whose brains are undergoing more substantial waking synaptic changes.
- ▶ Melatonin should be useful in the treatment of epilepsy.



There is a very close relationship between epilepsy and sleep that has been recognized since antiquity.

(Dinner and Lüders, 2001, first sentence)

Quality sleep is essential for patients with epilepsy, but this aspect of their treatment is frequently overlooked. Sleep disturbance can result in daytime drowsiness, worsening memory, and deteriorating seizure control. In a few patients, recognition and treatment of a coexisting sleep disorder can make the difference between complete seizure control and refractory epilepsy.

Sleep and Epilepsy (Bazil, 2002)

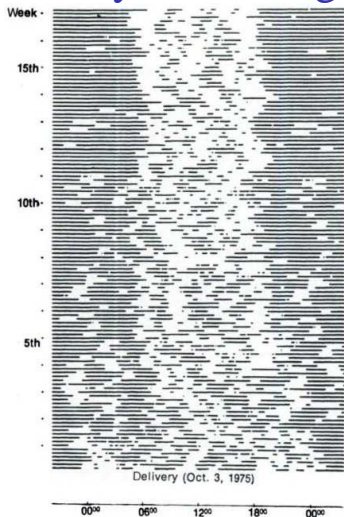
Sleep and Epilepsy

We all know that we think more clearly, react more quickly, and generally perform better after a good night's sleep. And while a good night's sleep plays a key role in the overall well-being and health of all people it is even more vital in people with epilepsy. One reason why is because a lack of sleep or poor quality of sleep can in turn increase frequency of seizures. The reasons why sleep deprivation provokes seizures are unclear.

http://www.epilepsy.com/epilepsy/sleep_epilepsy



Human Circadian Rhythm during Development



Double raster plot of sleep-wake patterns for one child from age 0 to 110 days, with dark bars indicating sleep. Sleep was judged by amount of activity. (From Meier-Koll et al., 1978)

Summary

The core function of sleep is to prevent uncontrolled neuronal feedback while allowing the brain to operate near the boundary of criticality.

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In a Nutshell I

- ▶ Big Mystery: SLEEP and TIREDNESS
- ▶ Big Idea: *The critical function of sleep is to prevent uncontrolled neuronal feedback while allowing rapid responses and prolonged retention of short-term memories.*
- ▶ Brain is efficient when:
 - ▶ Integrate sensory stimuli widely separated in time.
 - ▶ Many memories stored.
 - ▶ Rapid response, rapid retrieval.
 - ▶ I.e., nearly critical (in the dynamic systems sense)
- ▶ Small changes in the parameters or conditions can lead to runaway oscillations.
- ▶ The very changes that improve the processing performance of the network can put it at risk of runaway oscillation!

In a Nutshell II

- ▶ Stimulus-dependent plasticity should only be permitted when there is a margin of safety around the current network parameters.
- ▶ Proposal: a critical role of sleep is to establish a margin of safety by exposing the network to a variety of conditions and inputs, observing for erratic behavior, and adjusting the parameters accordingly.
 - ▶ During wakefulness this margin of safety is gradually consumed, ultimately requiring refreshment by another period of sleep.
 - ▶ When sleep is not possible, an emergency mechanism comes into play to prevent runaway oscillations at the expense of processing efficiency: tiredness.