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Sleep dynamics: A self-organized critical system

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In psychiatric and neurological diseases, sleep is often perturbed. Moreover, recent works on humans and animals tend to show that sleep plays a strong role in memory processes. Reciprocally, sleep dynamics following a learning task is modified [Hubert *et al.*, Nature (London) **02663**, 1 (2004), Peigneux *et al.*, Neuron **44**, 535 (2004)]. However, sleep analysis in humans and animals is often limited to the total sleep and wake duration quantification. These two parameters are not fully able to characterize the sleep dynamics. In mammals sleep presents a complex organization with an alternation of slow wave sleep (SWS) and paradoxical sleep (PS) episodes. Moreover, it has been shown recently that these sleep episodes are frequently interrupted by micro-arousal (without awakening). We present here a detailed analysis of the basal sleep properties emerging from the mechanisms underlying the vigilance states alternation in an animal model. These properties present a self-organized critical system signature and reveal the existence of two W, two SWS, and a PS structure exhibiting a criticality as met in sand piles. We propose a theoretical model of the sleep dynamics based on several interacting neuronal populations. This new model of sleep dynamics presents the same properties as experimentally observed, and explains the variability of the collected data. This experimental and theoretical study suggests that sleep dynamics shares several common features with critical systems.

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I. INTRODUCTION

Nowadays, sleep dynamics is considered as emerging from complex interactions between neuronal populations of many brain regions, located in hypothalamus and in brainstem. Indeed, until now, the alternation between sleep and wakefulness has been viewed as a sleep-wake "latch" system [1,2] or as a competition between neuronal populations [3,4] presenting mutual inhibitions. However, these kinds of systems providing cyclic rhythms do not present memory properties, and cannot evolve. In other words, they are not able to produce the large temporal variability observed in physiology. Consequently, they cannot exhibit exceptional events, as for instance a long or a very short wakefulness period. Recent works [5–7] tend to address a new concept of sleep dynamics based on the self-organized critical systems theory initiated in several physics domains by Per Back [8]. Interestingly, the wake and sleep duration and the recurrence interval of a vigilance state, that is the time interval between two consecutive episodes of the same nature (that we define as recurrence interval), follow a power-law $P(t) \sim t^{-\alpha}$ or exponential $p(t) \sim e^{-t/\tau}$ statistical distribution, called invariant and finite scale process, respectively. In contrast to works focused on the common scale-invariant patterns of sleep-wake transitions across mammalian species, we investigate in-depth the sleep architecture. The temporal sleep organization is more complex than is thought, because sleep is not restricted to a two states "wake-sleep" system. Indeed, the minimum number of states to describe the sleep architecture in mammals is equal to three. These states are named Wake (W), slow-wave sleep (SWS), and paradoxical sleep (PS) or rapid eye movement sleep (REMs), respectively. In humans, SWS is composed of four levels of SWS, implying a more complex sleep architecture. For the sake of clarity, we focus our attention on the best known animal model, the rat. Indeed, in the rat, the three above-cited states are sufficient to describe the sleep dynamics as represented Fig. 1(a). Note that the results of Ref. [6], indicating common behavior characteristics between species, allow us to extrapolate our results to humans. The present paper is organized as follows: In Sec. II, we present the experimental methods, while in Sec. III, we present our statistical investigations, and extract the properties of a basal sleep. Section IV presents a new theoretical model displaying the same properties as experimentally observed. Finally, Sec. V is devoted to some concluding remarks and possible future investigations.

II. EXPERIMENTAL METHODS

We analyze episode duration of the three sleep states W, SWS, and PS in a rat, during the diurnal period (the main sleeping period). The sleep states are scored following the electroencephalography (EEG), electromyography (EMG), and electrooculography (EOG) recordings (see Fig. 2). Our polysomnographic recordings have been performed with ten 24-h recordings from ten adult male Sprague-Dawley rats (weight: 300 g, age: 3 months) with 12-h period of light from 7 a.m. to 7 p.m. and constant temperature: 23 °C. Our data analysis is realized between 7 a.m. and 7 p.m. We adopt the usual experimental conditions and scoring criteria. Vigilance states were discriminated with the aid of EEG, EOG, and EMG recordings. Polygraphic recordings and sleep scoring EEG, EOG, and EMG recordings were collected on a computer via a CED interface using the Spike 2 software (Cambridge Electronic Design). The criteria used to distinguish between SWS, PS, and W were the following: wakefulness was characterized by a desynchronized EEG, PS was

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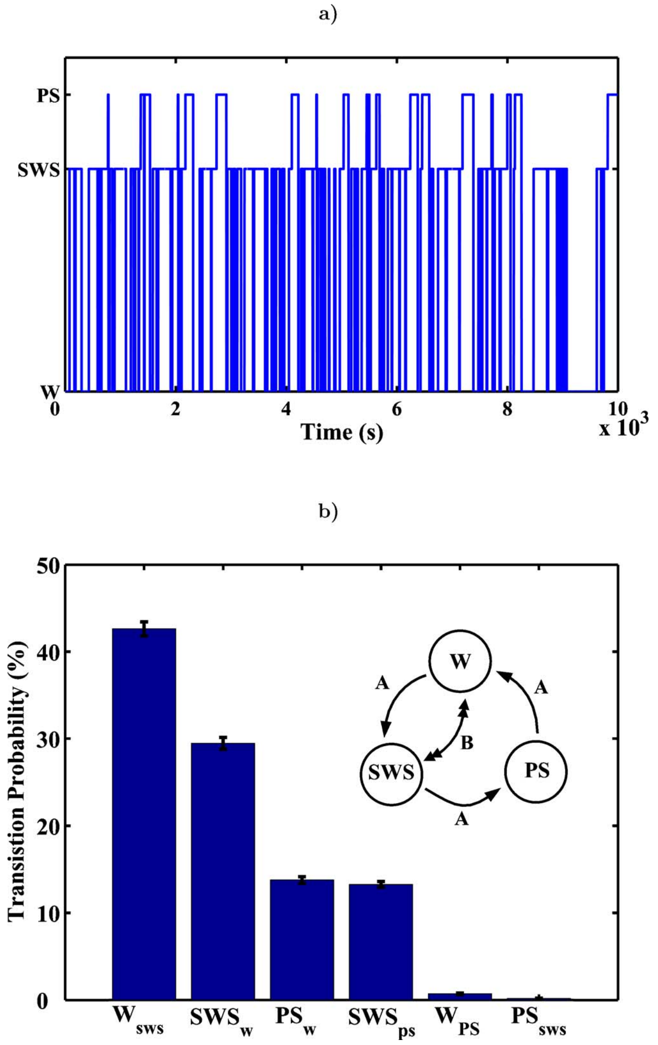

FIG. 1. (Color online) Sleep dynamics: (a) Typical hypnogram describing the sleep architecture of a rat during the diurnal period (sleeping period for the rat) represented over a period of 10^4 s for the sake of clarity and exhibiting six possible transitions between the three different states, PS (paradoxical sleep), W (wake), and SWS (slow waves sleep). (b) Transitions probabilities between vigilance states following a Pareto diagram, from which we can extract the main sleep trajectories A and B (represented upright). One notes, the very rare transitions W → PS and PS → SWS, and consistency (very low standard deviation) of the results obtained from 10 rats.

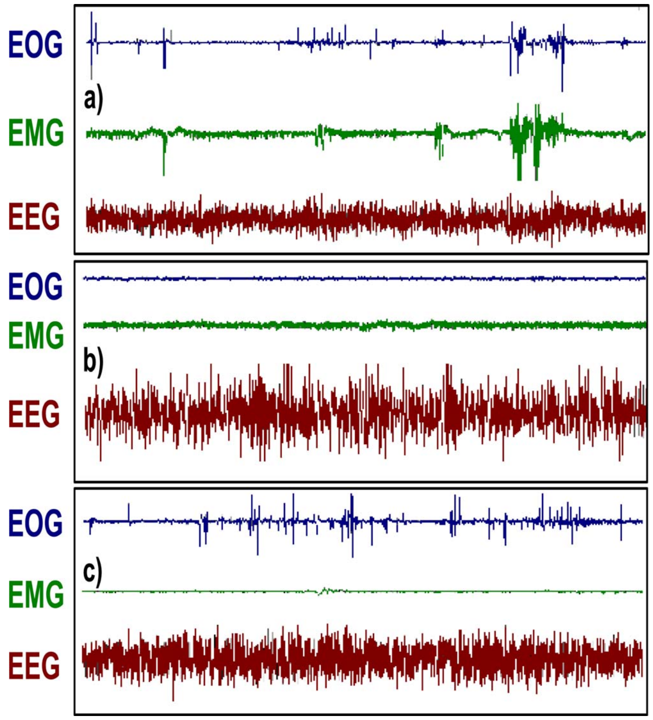

FIG. 2. (Color online) Polygraphic recordings of the three different vigilance states. (a) Wake state is associated with a weak EEG amplitude, a strong muscular tonicity, and a strong ocular activity. (b) Slow waves sleep is associated with a strong EEG amplitude, a reduced muscular tonicity, and no ocular activity. (c) Paradoxical or REM sleep is associated with an EEG, and EOG close to the wake state with no muscular tonicity.

characterized by a large increase in power of theta activity (4–8 Hz) accompanied by muscle atonia, and SWS was characterized by large amplitude delta oscillations (1–4 Hz) in the EEG. Sleep stages are scored by dividing sleep recordings into nonoverlapping epochs of the same duration. A single sleep stage is assigned for each epoch. Polygraphic recordings were analyzed with 5-s epochs. If more than one sleep stage occurs within an epoch, the majority sleep stage is scored as the stage for the whole epoch leading to an hypnogram as represented Fig. 1(a). Note that this scoring rule applied to a too large epoch analysis ($\geqslant 30$ s) leads to an hypnogram with artifacts giving rise to a Gaussian statistics in accordance with the central limit theorem. Thus, in order to extract the statistical properties of the sleep dynamics, it is important to choose an adapted time scale to analyze EEG, EMG, and EOG recordings. A systematic scale analysis reduction allowed us to determine the limit (5 s) under which it is useless to descend and over which the time resolution is damaged. We plot our data onto a three-state diagram (W, SWS, and PS).

III. STATISTICAL RESULTS

Sleep dynamics are characterized by two mains features: (i) the vigilance states alternation, (ii) the vigilance states duration. Thus, we have first performed the analysis of the transition probability between vigilance states. The transitions probability bargraph represented in Fig. 1(b) presents a Zipf-like power law (i.e., a power law between the probability versus the sorting rank emerging from a Pareto diagram), suggesting a critical character of the studied system. This analysis leads to identifying two sleep trajectories [see Fig. 1(b)]. The first trajectory links the W state to the SWS state, the SWS state to the PS state, and finally the PS state to the W state (cycle A). The second trajectory connects the W state to the SWS state and reciprocally (cycle B). One notes the very weak weight of the W to PS, and PS to SWS transitions. Sleep dynamics is not restricted to the transitions between vigilance states. Indeed, the actual sleep complexity resides in the vigilance states' duration. In order to extract the tem-

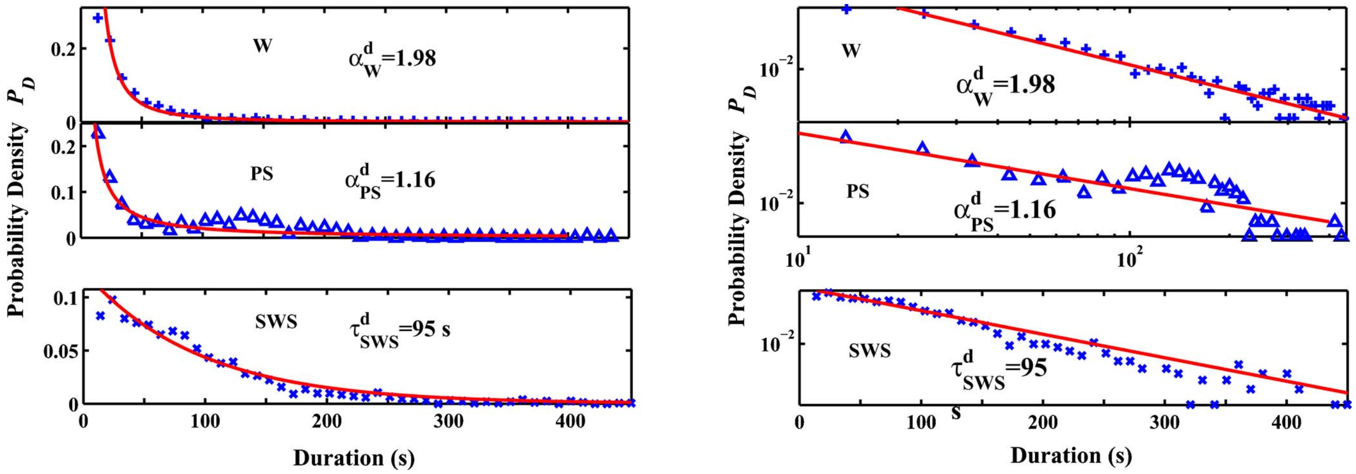

FIG. 3. (Color online) Episode duration probability density in linear plot (left side) and double logarithmic or semilogarithmic plot (right side): (W) probability density of the wake duration following a power law with a critical exponent $\alpha^d_W=1.98$, (SWS) probability density of the slow waves sleep duration following a decreasing exponential law presenting a constant time scale $\tau^d_{SWS}=95$ s. (PS) Probability density of the paradoxical sleep duration following a power law with a critical exponent $\alpha^d_{PS}=1.16$. Note the small hump in the tail related to the W to PS. Each probability density graph results from the hypnograms analysis of 10 rats during 12 h.

poral properties of the different vigilance states, we have performed statistical analysis of their duration, as shown in Fig. 3. The duration probability densities of W and PS states represented Fig. 3, follow a power law with critical exponents equal to $\alpha^d_W=1.98$ for W and $\alpha^d_{PS}=1.16$ for PS, respectively. These critical exponents are the slopes of the double logarithmic axis of the graph represented on the right side of Fig. 3. The SWS episodes duration distribution presents a decreasing exponential also called finite scale characteristic, indicating that the SWS duration scale is equal to $\tau^d_{SWS}=95$ s. This duration scale is determined by the slope of the semi-logarithmic data representation located on the right side of Fig. 3. In order to prove the robustness of our investigations, we have equally compared the individual characteristics of each animal with the merged data obtained for all animals. Figure 4 shows the properties of a randomly chosen animal matching accurately with the merged data obtained for all animals represented by the continuous lines.

Note that the nonparametric Kolmogorov-Smirnov test (which does not require the assumption that the population is normally distributed) applied to the data from individual recordings reveals that we cannot reject the null hypothesis that W, SWS, and PS states of each subject are drawn from the same distributions, suggesting that one can pool all data together to improve the statistics without changing the global distribution.

As shown in Fig. 1(b) representing the two possible sleep trajectories, two paths exist to reach the W state depending on whether the preceding vigilance state is a SWS or PS state (see Fig. 6). Also, two ways exist to leave the SWS state depending on whether the next vigilance state is a W or PS state (see Fig. 5). Thus, we have to construct the duration distributions of the W state when the preceding state is a SWS state or a PS state (see Fig. 6). Also, we have equally to construct the duration distribution of the SWS state when the next state is a W state or a PS state (see Fig. 5). One notes the presence of two distinct duration distributions for the W and the SWS episodes. The duration probability density of the W state is the combination of the power law distributions of critical exponents equal to $\alpha_{PS}=1.54$ and $\alpha_{SWS}=2$, de-

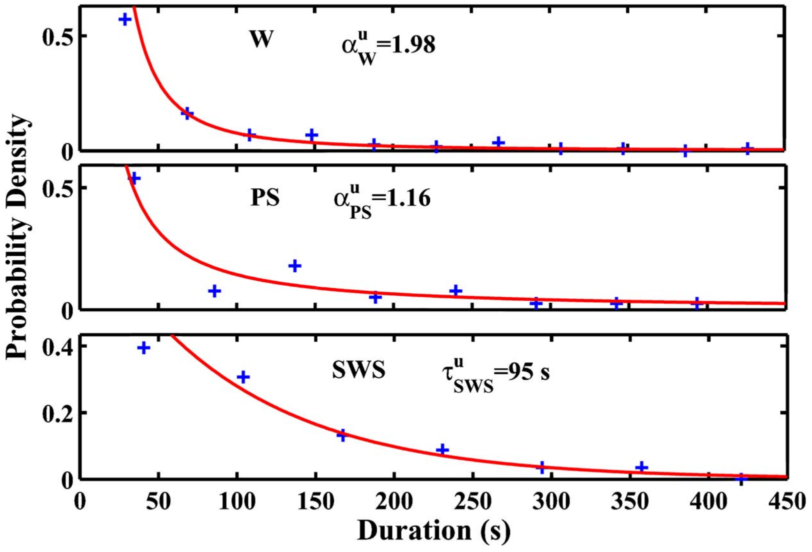

FIG. 4. (Color online) Statistical properties of a randomly chosen animal, compared to the merged data obtained for all animals. From top to bottom: probability densities of the wake (W), paradoxical sleep (PS), and slow waves sleep (SWS). The red curves represent the results from the data of Fig. 3 (all animals), superimposed to the data of a randomly chosen animal showing the results sturdiness.

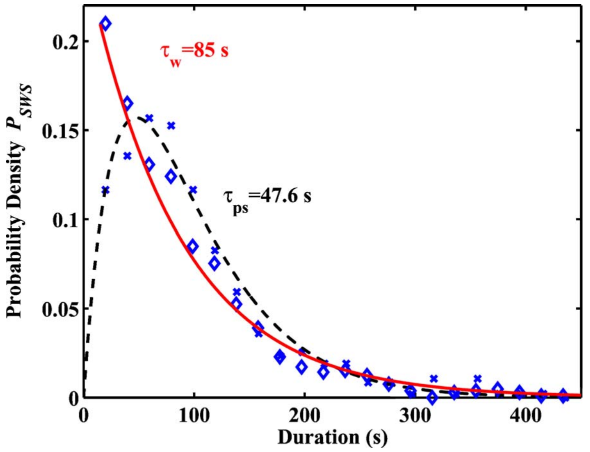

FIG. 5. (Color online) Duration probability density P_{SWS} of a SWS episode preceding a W (red curve, ◇) or a PS (black dashed curve, ×) episode. The red curve presents a time constant $\tau_w = 85$ s, while the black dashed one presents a time constant $\tau_{\mathrm{ps}} = 47.6$ s, indicating that two structures or mechanisms share the slow waves sleep state.

pending on whether one comes from a PS or SWS episode, respectively. The duration probability of the SWS state is the combination of an exponential and Poisson-like distribution of parameters $\tau_{\mathrm{W}} = 85$ s and $\tau_{\mathrm{PS}} = 47.6$ S, depending on whether SWS episodes are followed by a W or PS episode, respectively. Altogether, these results quantify some aspects of the sleep dynamics, in terms of duration and recurrence. Also, our results indicate that the classical proposed models based on a sleep architecture with mean duration and mean period are not appropriate to describe the actual temporal dynamics (variability) of vigilance states during sleep, and consequently lead to an erroneous interpretation of the sleep dynamics and therefore of its functions. Thus, the statistical analysis presented here suggests that the vigilance states' alternation during sleep emerges from a SOC system, like the paradigmatic sand pile model [8,9]. Indeed, a certain analogy exists between the location and the intensity of an avalanche in a sand pile and the vigilance state (location) and its duration (intensity), respectively, during a sleep period. The next section is devoted to a SOC model construction of the sleep architecture.

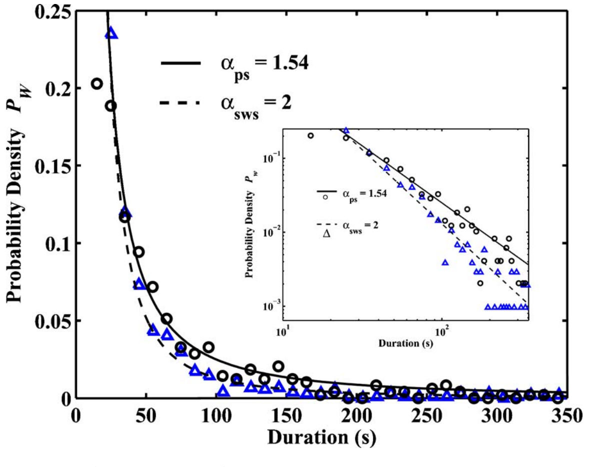

FIG. 6. (Color online) Duration probability density P_w of a wake episode following a SWS (dashed line, △) or PS (continuous line, ○) episode. Dashed line and continuous line presents a critical exponent equal to $\alpha_{\mathrm{sws}} = 2$ and $\alpha_{\mathrm{ps}} = 1.54$, respectively, indicating that two structures or mechanisms share the wake state. Inset: A double logarithmic representation shows the two straight lines characterizing the data power law properties.

IV. MODEL DESCRIPTION

Our statistical investigations described in Sec. IV show that the SWS episodes follow two different finite scale duration laws depending on the sleep trajectory (A and B see Fig. 1). Moreover, depending on the sleep trajectory, A or B, one distinguishes two different W duration power laws. The PS duration distribution presents a power law structure with a small hump located on the distribution tail. This small hump related to the rare W to PS transitions presents a mean duration equal to 120±10 s and does not play a crucial role in sleep dynamics because of its rarity and its small size in comparison with the whole of the duration distribution of PS, and consequently may be neglected in our model. These statistical results suggest that the vigilance states' alternation during sleep behaves as a SOC system similar to the paradigmatic sand pile model, where an episode of a vigilance state may be assimilated to an avalanche. The avalanche location may be viewed as the nature of the vigilance state (W, SWS, or PS), while the episode duration of the vigilance state may be considered as the avalanche intensity. Our statistical results described above (see Fig. 1) show that transitions between vigilance states (W → PS, and PS → SWS) are very rare and can be neglected in comparison with the other transitions. Moreover, we have shown that the duration distribution of the SWS episode before a PS episode is different from the duration distribution of the SWS episode before a W episode. In addition, we have shown that the W duration distribution is different and depending on the preceding episode is a SWS or PS a episode. From these results, we have constructed a SOC model with five neuronal populations (see Fig. 7). The populations responsible for the W state maintenance are labeled W and w, respectively, while the two populations responsible for the SWS state maintenance are labeled SWS and sws, respectively. Finally the population responsible for the PS state maintenance is labeled PS. At this step of the model description, we would like to underline that each neuronal population described above is associated to a vigilance state maintenance. The assumption of the present model is to consider that the above-described neuronal populations are not the single possible vectors of the vigilance states' alternation, since among a similar neuronal population we can find excitatory and inhibitory neurons, [10–12] and furthermore, as has been suggested in Refs. [13,14], neuromediators can play an inhibitory as well as excitatory role. Efferent arrows from a neuronal population (see Fig. 7) to others represent the possible neuronal population activation trajectories from the most active population. It is important to note at this level of description that the arrows of Fig. 7 are not probability weighted, and that transitions or neuronal population activation emerge from simple comparison of neuronal populations activities (winner take

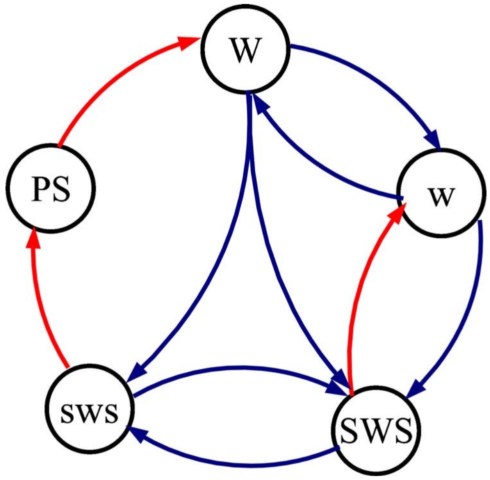

FIG. 7. (Color online) Transition map model between the different "neuronal species" implied in the sleep dynamics. One notes first the existence of two wake (w and W) and two slow waves sleep (sws and SWS) structures. This interaction ring network shows mutual interactions between two consecutive agents, except between the nodes sws, PS, and W, representing the paradoxical sleep way "A." Second, the nonparadoxical way "B" is a complex connections system, giving rise to the sleep self-organized criticality.

all). Neuronal populations' activity is obtained from a random pull for each neuronal population efferently connected by an arrow to the most active current neuronal population. Others neuronal populations (not efferently connected by an arrow) are considered to be hyperpolarized (by hormonal species, or neuromediators,…). In contrast to the current idea for which the vigilance states' alternation results from only mutual inhibitory and excitatory relationship between the neuronal populations involved in the sleep states' maintenance, the random drawing exposed above allows us to gather the role of the neuronal populations involved in the sleep states' maintenance and the rest of the brain. Indeed, neuronal populations in the brain are directly or indirectly connected to others far and/or close to neuronal populations. From this remark it is not possible to reduce sleep states' dynamics to mutual inhibitory and excitatory neuronal populations isolated from the rest of the brain. In the present model, other neuronal populations in the brain are considered as playing a strong role in the vigilance state alternation, since different areas can stimulate or inhibit the various neuronal populations responsible for a vigilance state maintenance. Moreover, our model also integrates the possible inhibitory and excitatory relationship between neuronal populations responsible for the sleep states' maintenance. Figure 8 shows the results of our numerical simulations which exhibit the same properties as experimentally observed. In particular, our model presents the same range order of critical parameters, the same time scale, as well as regarding the vigilance states' duration, as the transition probabilities. It is important to remember here that no transition parameter value has been incorporated in our model voluntary. These numerical results indicate that our SOC model exhibiting the same statistical properties as experimentally observed, is another way to model the sleep dynamics and allows one to characterize accurately the sleep architecture, and consequently is a genuine tool to determine the sleep functions. This model involves the notion of contingency between the conformation of the system (neuronal populations responsible for the maintenance of their corresponding vigilance state) and the intervention of a perturbation or excitation coming from other brain areas which can induce a strong change in the system conformation, whatever the perturbation size. This suggests that the sleep dynamics time course is not predictable. Only the statistical properties of SOC systems can be determined. The construction of a simple model including the most relevant ingredients of the sleep architecture allows one to compare the theoretical properties to the experimental ones and consequently to determine the mains characteristics of the studied system and how the different neuronal populations interact.

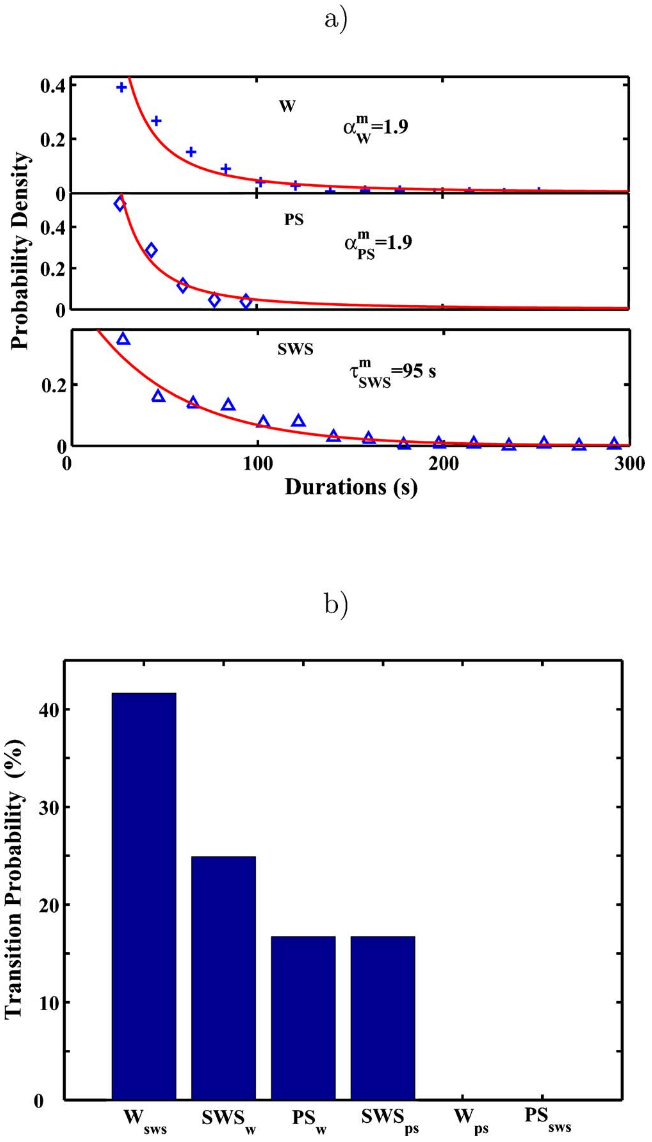

FIG. 8. (Color online) Statistical results obtained from numerical simulation of the proposed model. (a) Vigilance states duration probability density, displaying the same characteristics as experimentally observed $\alpha_W^m=1.9$, $\alpha_{PS}^m=1.9$, $\tau_{SWS}^m=95$ s. (b) Probability of transition between the different vigilance states, presenting the same range order as the experimental results [see Fig. 1(b)].

This model leads to a new concept of sleep working, in which all the brain is considered, unlike other sleep models [1–3].

V. DISCUSSION

In summary, we have shown in this article that the sleep dynamics in the best known animal model of sleep share many similarities with a typical SOC system. Indeed, in mammals, sleep has a complex architecture which involves a minimum of three vigilance states W, SWS, and PS. In contrast to the early descriptions of sleep cycle [15] the analysis of hypnograms in animals and in humans with short epochs has revealed the frequency of very short (<1 min) episodes of PS and W during sleep. Sleep, as critical systems, exhibits invariant or finite scale behaviors meaning that big and small events have the same significance. Our results indicate that these short episodes are not a noise superimposed to a basic periodic pattern. The fact that sleep dynamics shares many similar features with SOC systems is important in terms of understanding system biology. Indeed this temporal organization of sleep should be split from the circadian and respiratory rhythms which are strictly periodic. Although our results are based on experiments in the rat, the study of Lo [6] allows us to extrapolate our findings to other species, including humans. Frequently it has been hypothesized that the neuronal populations underlying these rhythms may share similar pacemaker mechanisms. In contrast, our results suggest that the neuronal populations involved in sleep present a different behavior. These temporal analyses combined with the analysis of the transition probabilities between vigilance states allowed us to construct a critical theoretical model of the activity of neuronal populations underlying the vigilance state induction and maintenance. First, our model presents the same statistical properties of the sleep dynamics; that is: the same duration of vigilance state episodes and recurrence interval variability, as well as the same distribution transition probabilities between vigilance states. Thus, this model which is a new way to accurately describe sleep dynamics is able to exhibit the variability and the statistical distributions experimentally observed. The second main feature of this model is that the activity of a neuronal population responsible for a vigilance state maintenance contributes to the inhibition of the other neuronal populations associated with the other vigilance states. Thus the current active neuronal population is not the only population that contributes to the vigilance state maintenance. Indeed, our model suggests that the vigilance states' alternation depends mainly on events coming from other neuronal populations located in brainstem and hypothalamus or even other brain areas which activate or inhibit these populations responsible for the vigilance states' maintenance. One can compare these neuronal interactions to a sand grain which falls on a sand pile in critical regime. Depending on where the grain falls this one excites a chain of force and triggers or does not trigger an avalanche in a certain area of the sand pile. In this comparison, the sand grains play the role of the neurons, the chain of forces represent the neuronal arborescent of the active neurons of the rest of the brain in the direction of the populations responsible for the vigilance states' maintenance. Recently it has been demonstrated that the propagation of activity in *in vitro* neuronal networks behave as a sand pile system [16]. Our theoretical results suggest that such complex neuronal interactions between different brain areas may underlie the complex temporal architecture of sleep. This remarkable similarity between neuronal interactions in the brain and the sand pile is also interesting in terms of experimental support and theoretical description. However, like in a sand pile, where it is not possible to determine the next avalanche location and intensity, the prediction of the activation of the next neuronal population and its duration are not possible. Thus, the sleep dynamics is driven by a critical state that may allow the optimum integration of much different information including body temperature, fasting, glycemia, brain reactivations after learning. Also, we suggest that the underlying mechanisms of the sleep temporal organization result from the synchronous activation or deactivation of the neuronal populations of different brain areas (coding for temperature, glycemia, etc.), not only from the activation of the classical neuronal populations involved in sleep maintenance and induction.

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