Self-Organized Criticality and Dynamic Instability of Microtubule Growth

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We have shown that the distribution of lengths of site nucleated microtubules obey an algebraic power law relationship $D(s) = A\,s^{-\tau}$, where $D(s)$ is relative number of microtubules with length s, A and τ are constants. This relationship indicates the possibility of a self-organized criticality in the dynamic instability of microtubule growth.

One of the simplest self-assembling structures found in biological systems are the microtubules, one of the fundamental components of the eukaryotic cytoskeleton and the primary structural elements of cilia and flagella (Garret and Grisham, 1995).

Individual microtubules reassembled from purified tubulin undergo alternating phases of elongation and rapid shortening (Mitchison and Kirschner, 1984; Walker *et al.*, 1988). The transition (catastrophe) from elongation to shortening, and the reverse transition (rescue) are abrupt and apparently stochastic. This behavior known as dynamic instability was observed also in living cells (Cassimeris *et al.*, 1988). Switching between growing and shrinking states at constant concentration of free tubulin is very unusual for a polymer. The molecular basis of dynamic instability is still an unresolved problem. The key element of many proposed models (Erickson and O'Brien, 1992; Flyvbjerg *et al.*, 1994) is the competition between growth and GTP hydrolysis. The growing microtubule has a stable cap of GTP tubulin and if hydrolysis overtakes addition of new GTP tubulin, destruction of the cap leads to microtubule disassembly.

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An enormous variety of systems in physics, chemistry and biology seems to exhibit scale invariance in some form or another (Mandelbrot, 1982). Our aim is therefore to analyze the possibility that such behavior take place also in microtubule growth dynamics. In mathematical form scale invariance means that the distribution function is described by the algebraic power law relationship

$$D(s) = A\,s^{-\tau}, \tag{1}$$

where $D(s)$ is relative number of microtubules with length s, A and τ are two constants.

Taking decadic logarithm on both sides of this equation we get

$$\log D(s) = \log A - \tau \log s. \tag{2}$$

By plotting $\log D(s)$ *versus* the $\log s$, a straight line should be obtained. From slope and axis intercept, the constants τ and A can be obtained.

Lengths of microtubules are ranging from 10^{-3} μm to 10^{2} μm. Distribution of the lengths of microtubules was recently studied by differential – interferometry contrast microscopy (Fygen-

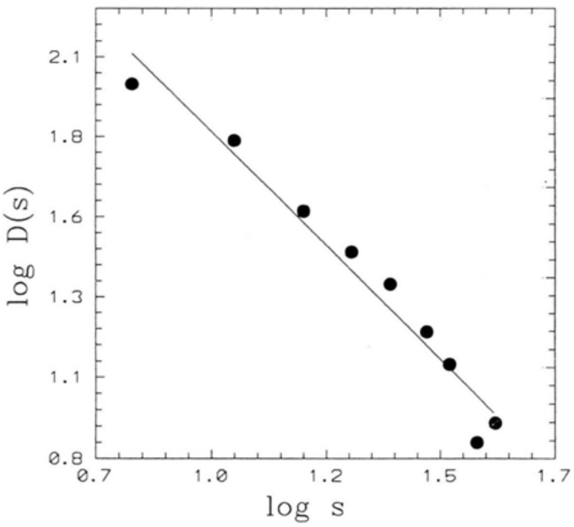

Fig. 1. Double logarithmic plot of the microtubule length distribution function $D(s)$ at 14.4° C for 45 μM tubulin concentration (data taken from Fygenson *et al.*, 1994). The straight line is a least-squares fit to the data. The $\log s$ and $\log D(s)$ denote decadic logarithms of s and $D(s)$, respectively. $D(s)$ is the relative number of microtubules with the length s.

son *et al.*, 1994). Using their data (Fig. 1) we have found values $\tau \cong 1.42$ and $A \cong 1450$.

This behavior is the main feature of the recently proposed concept of self-organized criticality (SOC) (Bak *et al.*, 1988), a new paradigm for understanding complicated dynamical systems, where many parts influence each other with a short range interaction. It was proposed that such a system will naturally evolve to a critical state where small perturbations could lead to either minor or catastrophic events. The SOC concept has been recently applied to such diverse areas like e.g. high-temperature superconductivity (Wang and Shi, 1994), biological evolution (Bak and Sneppen, 1994) and neurobiology (Babincová and Babinec, 1995).

Another "fingerprint" of SOC is the spatial self-similarity, which has been also recently observed (Tabony, 1994) in spontaneously created pseudo-helical microtubular bands.

Microtubules participate in a wide variety of dynamic processes in the cell, which rely on their ability to change efficiently their organization (Holy and Leibler, 1994). This ability may be very naturally a result of SOC, where two events correlate whether or not they occur close to each other in space and irrespective of the time interval between them. Analogous to this situation are phase changes of the matter, e.g. if the gas condenses to form a liquid, the positions and motions of atoms are similar in this critical state and affect each other over all distances.

Cell biologists have invested considerable effort to understand the process of microtubule assembly, mainly in terms of linear phenomena. The present result suggest that such complex biological phenomena may occur as a result of nonlinear nonequilibrium mechanisms (Hess and Mikhailov, 1994).

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