PSYCHOPHYSICS

Are our senses critical?

The sensitivity and dynamic range of a network made of neuron-like elements is now shown to be maximized at the critical point of a phase transition. This raises the question of whether critical senses might improve survival in a critical world.

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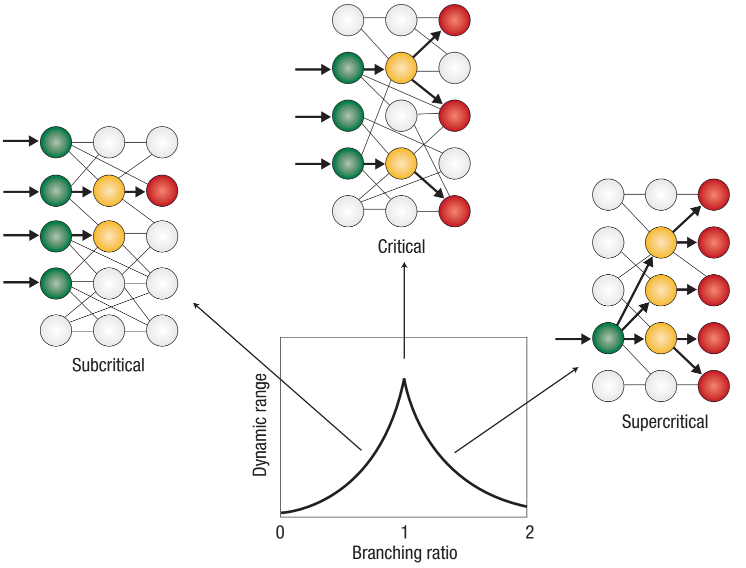

Figure 1 Be critical. Networks constructed with branching ratios close to one maintain, on average, the input activity (green, followed by yellow and red), thus optimizing the dynamic range. Instead, supercritical networks explode with activity, whereas subcritical ones are unable to sustain any input pattern.

A century and a half ago, the field of 'psychophysics' was born in Leipzig, when physicist Gustav Fechner and physiologist Ernst Weber sought to assign numerical values to the human response to a physical stimulus. Those already familiar with this early marriage between soft and hard sciences will now welcome the elegant solution to one of the oldest unsolved problems in this field, which Kinouchi and Copelli present on page 348 of this issue[1]. They provide a physical explanation for the ability of our senses to respond with similar ease to both minuscule and enormous changes in our surroundings. This performance implies equal sensitivity over an extremely wide dynamic range, something that is not easily attained even for scientific instruments. For example, we can hear sound pressures in a range of intensities covering twelve decades, and perceive changes in about ten decades of luminosity. Other senses have similar abilities. However, it is known that an isolated neuron-like element — the basic building block from which our senses are constructed — can encode only signals spanning a single order of magnitude. It is therefore not easy to understand how these tremendously large dynamic ranges are achieved.

A century-old accumulation of data relating sensation intensity S and stimulus magnitude I, estimated for many sensory modalities, can be condensed to the single nonlinear relation $S \propto I^{\alpha}$, now known as the Fechner–Weber–Stevens law. The exponent α determines the 'transfer function' between stimulus and sensation. The unsolved problem is the neuronal mechanism giving rise to such exponents; in other words, what is the physics of the psychophysics?

Kinouchi and Copelli[1] claim that the dynamics emerging from the interaction of coupled excitable elements bears the key to the problem. Their results show that a network of excitable elements set precisely at the edge of a phase transition — or, at criticality — can be both extremely sensitive to small perturbations and still able to detect large inputs without saturation. This is generic for these networks regardless of the neurons' individual sophistication or simplicity. Physicists familiar with, say, the high susceptibility found in a ferromagnetic–paramagnetic phase transition at the critical temperature will not have problems agreeing, in principle, with this notion, but still will wonder how this scenario would be in the realms of neurobiology.

To set up a neuronal network at criticality, the key point is to ensure — by some mechanism — that the ratio of future activity to past activity remains close to unity. This ratio is a measure of how activity branches out, and is thus known as the 'branching ratio'. To be more specific, a branching ratio of one means that if at any given time t you observe N neurons firing, you should count, on average, N active neurons at time $t + 1$ (Fig. 1). Kinouchi and Copelli chose to model these branching conditions by treating a neuron as a simple cellular automaton, and randomly coupling each neuron to a handful of other neurons. If you set the model up with a branching ratio smaller than one, and run several iterations, activity dies out: the model

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is subcritical and not sensitive to small inputs. On the other hand, if you choose a branching ratio larger than one, this sets up the conditions for a supercritical reaction, in which the entire network fires for even very small inputs (Fig. 1).

The latter two cases are clearly inadequate to model how our senses work: in the subcritical setting, the network has an inappropriate sensitivity to small inputs, whereas in the supercritical case, the system quickly saturates. It is only when the branching ratio is close to one that the system shows the performance seen across our sensory systems. Under these conditions, the number of neurons engaged by any stimulus remains proportional to the intensity of the stimulus. As a consequence, the system is able to encode small and large inputs with the same fidelity, and the dynamic range is limited in principle only by the size of the network, and not by the properties of the individual neurons. When the dynamic range is explicitly calculated for a wide range of branching ratios, a clear optimum emerges for a branching ratio equal to one, indicating that criticality gives the best performance for such networks.

The basic results of the study of Kinouchi and Copelli are robust and independent of the details of the neuron model, as long as the branching ratio and certain aspects of the network connectivity are preserved. In that respect, it seems safe to speculate that similar results will be obtained from networks constructed from a variable number of excitatory and inhibitory units, which are known to spontaneously show critical dynamics, as recently shown experimentally in cortical networks[2].

The main suggestion of the findings by Kinouchi and Copelli is that, to be sensitive to the widest range of intensities, the neuronal network supporting our senses must be critical. Since these senses allow animals to survive, to gather food, to find mates, and to escape predators, one might ask what the evolutionary pressure was that pushed the sensory machinery to become critical. When you realize that ‘senses’ are the various ways that animal cells have found useful for converting the energy dissipated in our environment, then the answer seems rather simple: senses are critical because we evolve and live in a critical world. As pointed out repeatedly by Bak and colleagues[3–5], it is only in a critical world that energy is dissipated in space and time as a fractal, with characteristic highly inhomogeneous fluctuations. An animal in a subcritical world would not make any use of sensors with large dynamic range, because everything would be equally steady and frozen; indeed, it is hard to conceive of life itself existing under such conditions. Going to the other extreme, sensors would be useless in a supercritical world, because things would be changing too fast all the time. Instead, in the real world, senses are needed to gather information from a wide range of energies, where nothing is steady and uniform, where extreme events exist, and where probabilities often have long tails. In the real (critical) world, the fresh smell of a new day, or the heavy perfume of lilies in warm, humid summer air can be suddenly interrupted by strong heavy smoke from a nearby forest fire, in the (necessarily critical) cycle of getting and dissipating energy. As the world around us appears to be critical, it seems that we, as evolving organisms embedded in it, have no better choice than to be the same.

REFERENCES

1. Kinouchi, O. & Copelli, M. *Nature Phys.* **2**, 348–352 (2006).
2. Beggs, J. M. & Plenz, D. J. *Neuroscience* **23**, 11167–11177 (2003).
3. Bak, P., Tang, C. & Wiesenfeld, K. *Phys. Rev. Lett.* **59**, 381–384 (1987).
4. Bak, P. & Paczuski, M. *Proc. Natl Acad. Sci. USA* **92**, 6689–6696 (1995).
5. Bak, P. *How Nature Works: The Science of Self-Organized Criticality* (Oxford Univ. Press, Oxford, 1997).

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