The structure of consciousness

Subjective awareness may depend on neural networks in the brain supporting complex wiring schemes and dynamic patterns of activity.

György Buzsáki

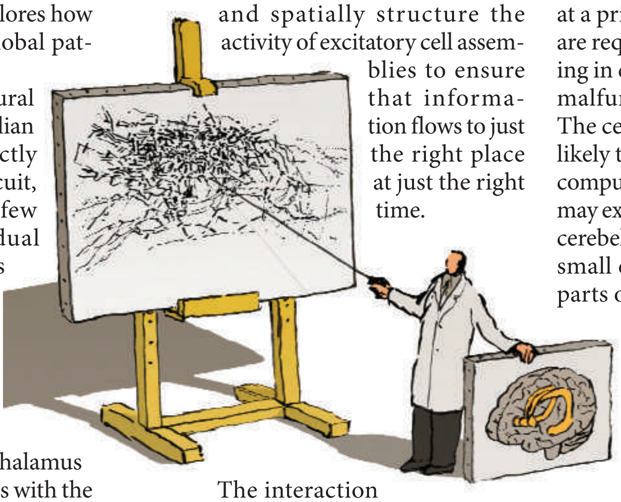
Perhaps nowhere is the truism 'structure defines function' more appropriate than for the brain. The architecture of different brain regions determines the kinds of computations that can be carried out, and may dictate whether a particular region can support subjective awareness. Also, the degree of architectural complexity may determine susceptibility to neurological and psychiatric diseases — complex architectural schemes being more prone to disruption than simpler ones. Understanding how such structure–function relationships govern brain operations requires a systems-level approach that explores how local computation relates to global patterns of neural activity.

At least three basic architectural schemes are present in mammalian brains. The simplest uses strictly local wiring. In this kind of circuit, typified by the cerebellum, a few neuronal types form individual 'modules' that may be repeated as necessary. Because interaction between modules is restricted to neighbours, it is massively parallel in nature. In different species, the size of locally organized brain structures — including the basal ganglia, thalamus and cerebellum — roughly scales with the number of modules they contain.

An entirely different type of network uses random connections, with a more or less equal probability of connecting local, intermediate or distant neurons. A unique example of such a random connectionist scheme is the recurrent excitatory circuit of the hippocampal CA3 region.

The third architectural scheme, exemplified by the neocortex, combines local modularity with more random, long-range connectivity. This complex wiring scheme shares many properties with 'small-world' or 'scale-free' networks. The advantage of this arrangement is that the number of intermediate steps between any two neurons — the synaptic path length — can remain relatively constant when network size is scaled up, because even a small fraction of long-range connections can dramatically reduce the average path length. Although intermediate and long-range interconnections demand resources and space, they are critical for globally distributing the results of local computations throughout the entire cerebral cortex.

I propose that the distinct network architectures translate into unique functional consequences. In cortical networks, a dynamic balance between excitation and inhibition gives rise to an array of network oscillations involving neuronal populations of varying sizes. This self-organized, or so called 'spontaneous' activity is the most striking and yet perhaps least appreciated feature of the cerebral cortex. Without inhibition, excitatory activity caused by any one stimulus would ripple across the entire neuronal network and a confused jumble of overlapping signals would result. Inhibitory interneurons and the rhythms they generate can temporally and spatially structure the activity of excitatory cell assemblies to ensure that information flows to just the right place at just the right time.



J. KAPUSTA/IMAGES.COM

The interaction and interference of multiple brain rhythms often gives rise to the appearance of 'noise' in an electroencephalogram. This noise is the most complex type known to physics and reflects a metastable state between the predictable behaviour of oscillators and the unpredictability of chaos. Neural firing patterns are thus controlled not only by the external sensory environment but also by the internally generated and perpetually changing state of cortical networks. Because local computation can be sensed by large parts of the cortex through long-range connections, and is also modified by this background 'noise', the term 'local–global computation' best captures the nature of cortical operations. A special case is the hippocampus whose highly recursive connection matrix is thought to function as a large 'autoassociator', allowing the reconstruction of entire episodes from remembered fragments.

I suggest that the local–global wiring of the cerebral cortex and the perpetual, self-organized complex dynamics it supports are necessary ingredients for subjective experiences. Environmental inputs can be seen as perturbations of the ongoing spontaneous activity. If they manage to perturb ongoing activity for a sufficiently long time in a big enough population of neurons, their effect will be noticed; that is, we will become conscious of them. In contrast, the locally organized cerebellar cortex, used largely for sensorimotor integration, does not give rise to self-generated or spontaneous activity, and its response to input remains local and non-persistent. Importantly, we generate no subjective record of such local computations.

Complex neuronal networks are a useful product of brain evolution but come at a price. Greater resources and volume are required to sustain long-distance wiring in complex networks, and the risks of malfunction increase with complexity. The cerebellar-type local organization is likely to be robust because errors in local computation are not disseminated, which may explain why functional diseases of the cerebellum are relatively rare. In contrast, small errors can propagate across large parts of complex networks and perhaps even be magnified by the rhythm-regenerating properties of the cerebral cortex. Timing errors present particularly difficult problems in complex networks, because of limits to how much information can be conveyed through restricted numbers of long-range conduits. Not surprisingly, diseases of the cerebral cortex are manifold — including epilepsies, Alzheimer's and schizophrenia.

One of the greatest challenges left for systems neuroscience is to understand the normal and dysfunctional operations of the cerebral cortex by relating local and global patterns of activity at timescales relevant for behaviour. This will require monitoring methods that can survey a sufficiently large neuronal space at the resolution of single neurons, and computational solutions that can make sense of complex interactions. ■

György Buzsáki is at the Center for Molecular and Behavioral Neuroscience, Rutgers University, 197 University Avenue, Newark, New Jersey 07102, USA.

FURTHER READING
Tononi, G., Sporns, O. & Edelman, G. M. *Proc. Natl Acad. Sci. USA* **91,** 5033–5037 (1994).
Buzsáki, G. *Rhythms of the Brain* (Oxford Univ. Press, 2006).

For other essays in this series, see http://nature.com/nature/focus/arts/connections/index.html