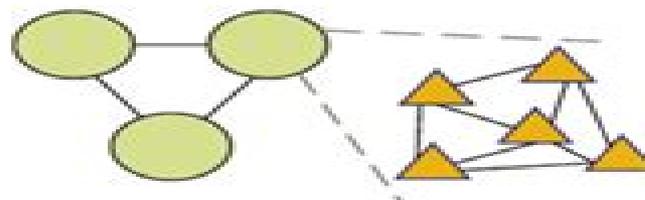


# Brain power

Vijay Balasubramanian<sup>1,2</sup>

The human brain is just 2% of the body's weight, but 20% of its metabolic load (1–3), and 10 times more expensive per gram than muscle. On the other hand, the brain manages to produce poetry, design spacecraft, and create art on an energy budget of ~20 W, a paltry sum given that the computer on which this article is being typed requires 80 W. So where in the brain is power consumed, what is it used for, why is it so expensive relative to other costs of living, and how does it achieve its power efficiency relative to engineered silicon? Many classic papers have studied these questions. Attwell and Laughlin (4) developed detailed biophysical estimates suggesting that neural signaling and the postsynaptic effects of neurotransmitter release combined to account for 80% of the brain's adenosine triphosphate (ATP) consumption, conclusions that are also supported by the overall physiology and anatomy of neural circuits (5, 6). Numerous studies explored the structural and functional consequences of this expenditure for limiting brain size (7) and scaling (8), efficient wiring patterns (9), analog (graded potential) vs. digital (spiking) signaling (10), distributed neural codes (11–13), the distribution of information traffic along nerve tracts and their size distribution (14–16), and computational heterogeneity and efficiency (17). Many of these ideas have been synthesized by Sterling and Laughlin (18) into a set of principles governing the design of brains. Now, in PNAS, Levy and Calvert (19) propose a functional accounting of the power budget of the mammalian brain, suggesting that communication is vastly more expensive than computation, and exploring the functional consequences for neural circuit organization.

Levy and Calvert (19) build on the earlier literature by focusing primarily on the relative power committed to different modes of information processing in the human brain, rather than on different aspects of cellular function. They make a key distinction between communication and computation. “Communication” refers, in general, to the transport of information, perhaps encoded in some way, from one site to another without



**Fig. 1.** Computation in the brain is distributed among specialized components communicating in networks. Green circles denote a network of cortical areas, each executing different functions. Orange triangles denote a network of pyramidal cells coordinating to compute the function of one cortical area. Levy and Calvert (19) argue that the cost of computation by the elementary units is dwarfed by the cost of communication between them.

transformation of the representation, extraction of salient features, or mapping to decisions or outcomes. An example in the brain is the transport of visual information, unchanged, along the optic nerve from the eye to the central brain. “Computation,” a more subtle concept, is generally understood in terms of an input-output transformation. Levy and Calvert, building on previous work of Levy, view each neuron as performing a “microscopic estimation or prediction” of latent variables in its input and encoding this output in interspike intervals (IPIs), that is, in the relative timing of the action potentials used in signaling by most neurons. Estimation and prediction are sufficiently general frameworks to subsume other views of neural computation (e.g., neurons as dynamical systems or logic gates), and also to encompass the role played by single neurons within networks charged with carrying out a computational function. Likewise, information coding in IPIs includes other possibilities like rate codes and pattern codes as specific cases. Thus, an example of a “computation” by a neuron in the brain could be

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See companion article, “Communication consumes 35 times more energy than computation in the human cortex, but both costs are needed to predict synaptic number,” 10.1073/pnas.2008173118.

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