

ters who gets them. Ecosystems tend to be owned by somebody, either privately or by the state (exceptions being deep oceans, the atmosphere, and Antarctica). Management decisions tend to reflect the interests of the owners, and where services demand other forms of capital (such as agricultural infrastructure), the supply of services depends on the availability of financial capital from owner, state, bank, donor, or investor. For example, in the Panama basin example discussed above (12), timber production and carbon sequestration increase or decrease together, but the two services have different beneficiaries in different locations. Land-owners have a direct interest in the private

**“...a monetary valuation of nature should be accepted only where it improves environmental [and] socioeconomic conditions...”**

benefits from either timber harvesting or livestock grazing, whereas carbon sequestration is a global public good. Choices about ecosystem management often involve such trade-offs between one service and another and between beneficiaries.

**LOSERS AND WINNERS.** Trade-offs among stakeholders in their access to ecosystem service benefits is a particular problem where there are differences in wealth and power. In the example of the Phulchoki Forest (Nepal) discussed above, community control of forest gave the local community the benefits of clean water, tourism, and harvested wild goods but restricted poor people's access to forest products, particularly those from certain “untouchable” castes. This created hardship, illegal use, and impacts on other areas (13).

Patterns of winners and losers from ecosystem services (and associated payment schemes) reflect prevailing patterns of wealth and power. Unequal access to ecosystem service benefits, including those experienced locally and at a distance, can lead to conflict, institutional failure, and ecosystem degradation. Institutional transparency, access to information, and secure resource tenure are fundamental to equitable outcomes.

**CONSERVATION/ECOSYSTEM SERVICES.** The identification and valuation of ecosystem services are valuable for sustainable environmental planning. Win-win outcomes are possible in cases where valuable ecosys-

tem services increase support for biodiversity conservation. Although areas of high biodiversity and those providing ecosystem services do not always overlap, improved conservation planning could help identify opportunities for win-win outcomes (14). However, the ecosystem service approach is not itself a conservation measure. There is a risk that traditional conservation strategies oriented toward biodiversity may not be effective at protecting ecosystem services, and vice-versa. Analysis using political ecology and ecological economics suggests that a monetary valuation of nature should be accepted only where it improves environmental conditions and the socioeconomic conditions that support that improvement (15).

The challenges described here suggest that considering conservation in economic terms will be beneficial for conservation when management for ecosystem services does not reduce biotic diversity or lead to substitution of artificial or novel ecosystems, when effective market-based incentives stimulate and sustain the conservation or restoration of biodiversity, and when the distribution of services among stakeholders favors high-diversity ecosystem states and is not undermined by inequality.

In a world run according to an economic calculus of value, the survival of biotic diversity depends on its price. Sometimes calculation of ecosystem service values will favor conservation; sometimes it will not. Conservationists must plan for both outcomes, rather than hoping that recourse to economic valuation will automatically win the argument for biodiversity. Ultimately conservation is a political choice (16), and ecosystem service values are just one argument for the conservation of nature. ■

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#### NEUROSCIENCE

## The atoms of neural computation

Does the brain depend on a set of elementary, reusable computations?

By Gary Marcus,<sup>1</sup> Adam Marblestone,<sup>2</sup> Thomas Dean<sup>3</sup>

**T**he human cerebral cortex is central to a wide array of cognitive functions, from vision to language, reasoning, decision-making, and motor control. Yet, nearly a century after the neuro-anatomical organization of the cortex was first defined, its basic logic remains unknown. One hypothesis is that cortical neurons form a single, massively repeated “canonical” circuit, characterized as a kind of a “nonlinear spatiotemporal filter with adaptive properties” (1). In this classic view, it was “assumed that these...properties are identical for all neocortical areas.” Nearly four decades later, there is still no consensus about whether such a canonical circuit exists, either in terms of its anatomical basis or its function. Likewise, there is little evidence that such uniform architectures can capture the diversity of cortical function in simple mammals, let alone characteristically human processes such as language and abstract thinking (2). Analogous software implementations in artificial intelligence (e.g., deep learning networks) have proven effective in certain pattern classification tasks, such as speech and image recognition, but likewise have made little inroads in areas such as reasoning and natural language understanding. Is the search for a single canonical cortical circuit misguided?

Although the cortex may appear, at a coarse level of anatomical analysis, to be largely uniform across its extent, it has been known since the seminal work of neurologist Korbinian Brodmann a century ago that there are substantial differences between cortical areas. At a finer grain, the brain has hundreds of different neuron types, and individual synapses contain hundreds of different proteins (3). Duplication and divergence shape brain evolution (4), just as they do in biology more generally.

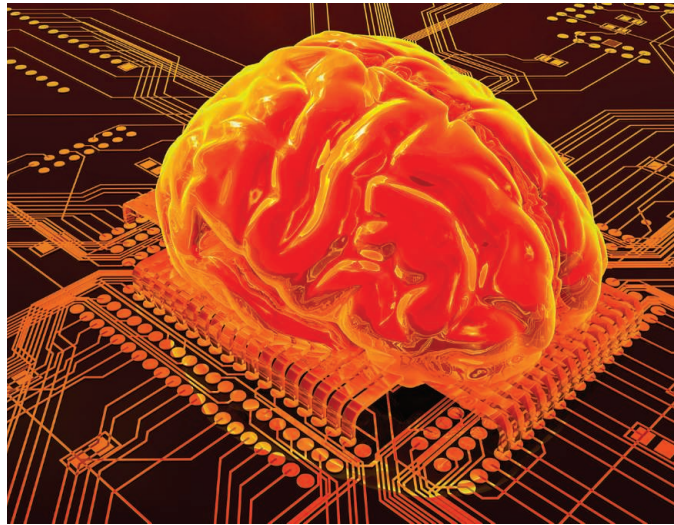
What would it mean for the cortex to be diverse rather than uniform? One pos-

sibility is that neuroscience's quarry should be not a single canonical circuit, but a broad array of reusable computational primitives—elementary units of processing akin to sets of basic instructions in a microprocessor—perhaps wired together in parallel, as in the reconfigurable integrated circuit type known as the field-programmable gate array.

Candidate computational primitives might include circuits for shifting the focus of attention (5), for encoding and manipulating sequences, and for normalizing the ratio between the activity of an individual neuron and a set of neurons (6). These might also include circuits for switching or gating information flow between different parts of cortex (7), and for working memory storage, decision-making, storage and transformation of information via population coding and the manipulation (2) and encoding of variables (8, 9), alongside machinery for hierarchical pattern recognition. Thus, cortical regions would differ not only in terms of their inputs, but also as a function of their inherent structures. The sensory cortex, for example, might be rich in circuits that underlie computational primitives useful for hierarchical pattern recognition and for mediating the effects of attention, whereas the prefrontal cortex might rely heavily on circuits supporting sequence production, decision-making, and variable binding.

Especially important in this regard (2, 10) is a greater understanding of the neural underpinnings of variable binding—the transitory or permanent tying together of two bits of information: a variable (such as an  $X$  or  $Y$  in algebra, or a placeholder like *subject* or *verb* in a sentence) and an arbitrary instantiation of that variable (say, a single number, symbol, vector, or word). Such processes appear to be outside the scope of uniform pattern recognition systems, yet are likely to be central both in language (e.g., in interpreting sentences that combine words in novel ways) and deductive reasoning. Variables likely figure prominently in other domains, as well, such as navigation, motor control, and higher-level vision (2, 10, 11).

Several candidate neural mechanisms for variable binding have been proposed. These range from temporal synchrony among neural ensembles (12), to multiplication of vec-



tors encoded by neural populations (9), to precisely controlled recurrent interactions between the prefrontal cortex and basal ganglia (8). Possible mechanisms also include interlinked systems of anatomically defined registers (groups of neurons defining temporary memory stores) with diverse encoding schemes (2, 11) that could be implemented through the combination of neurobiologically well-established processes (11), such as Hebbian learning (the idea that connections between two neurons are strengthened if the neurons are active simultaneously), gating, and attentional spotlights.

Relatively little experimental work, however, has focused on choosing among these possibilities, in part because earlier techniques (e.g., brain imaging studies) were too coarse-grained. Emerging techniques like optogenetics, which allows for the pinpoint control of individual neurons, in conjunction with activity mapping and scalable comprehensive maps of neuronal connections, give hope that specific questions about the microcircuitry of variable binding might soon be addressed. For example, it might be possible to identify microcircuitry involved in behavioral tasks that require the neural circuitry of variable binding (such as complex comparisons of multiple elements parsed from visual scenes), and then to perturb that circuitry through optogenetic techniques, yielding causal clues into the neural organization of the computational units underlying variable binding. Ultimately, an adequate account of the mechanisms of variable binding may be indispensable for drawing firm connections between neurons and higher-level cognitive processes.

Several recently discovered biological mechanisms could underwrite the development of a diverse set of computational building blocks, differentially arrayed across the cortex. For example, there are systematic

differences in gene expression between cortical areas, with differences between areas increasing as a function of their physical distance (13). Other molecular mechanisms, such as the alternative splicing of neurexins (proteins that help to orchestrate the formation of neuronal synaptic connections) (14), provide potential pathways by which seemingly subtle molecular differences could guide important qualitative variations in synaptic connectivity. Further, even within narrowly defined cell types (e.g., layer 5 pyramidal cells), molecularly defined combinatorial cues correlate with distinct patterns of wiring (15).

Neuroscience must develop precisely the sorts of experimental tools, detailed brain maps, and computational infrastructures that today's brain initiatives aim to support, but also a new set of intellectual tools for understanding how, even in principle, systems might bridge from neuronal networks to symbolic cognition. Toward that end, an interdisciplinary quest to construct a taxonomy and phylogeny of cortically instantiated computational primitives would advance our understanding toward the ultimate goal of deciphering how assemblies of such elements underlie behavior. ■

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