Cognitive Plasticity

Eduardo Mercado III

Cognitive Plasticity and Cortical Modules

Eduardo Mercado III

University at Buffalo, The State University of New York

Address correspondence to Eduardo Mercado III, Department of Psychology, Park Hall, University at Buffalo, The State University of New York, Buffalo, NY 14260; e-mail: emiii@buffalo.edu.

ABSTRACT—Some organisms learn to calculate, accumulate knowledge, and communicate in ways that others do not. What factors determine which intellectual abilities a particular species or individual can easily acquire? I propose that cognitive-skill learning capacity reflects (a) the availability of specialized cortical circuits, (b) the flexibility with which cortical activity is coordinated, and (c) the customizability of cortical networks. This framework can potentially account for differences in learning capacity across species, individuals, and developmental stages. Understanding the mechanisms that constrain cognitive plasticity is fundamental to developing new technologies and educational practices that maximize intellectual advancements.

KEYWORDS—cognitive neuroscience; comparative cognition; intelligence; cognitive aging; cognitive modifiability

Educated dolphins can answer questions about themselves and the world, improvise synchronized swimming routines on command, and correctly interpret symbolic instructions (Marino et al., 2007). What other skills might dolphins be able to learn given adequate schooling? More generally, what intellectual feats might any organism achieve if given optimal educational guidance? This question is difficult to answer because the neural and representational mechanisms that determine what skills an individual can learn or how rapidly learning can proceed remain essentially unknown. The purpose of this article is to describe how cortical structure, function, and adaptability may contribute to intellectual achievement. Understanding individual and species differences in learning capacity can potentially lead to ways to improve schooling techniques, ameliorate age-related cognitive decline, and rehabilitate patients with brain damage or dysfunction.

VARIABILITY IN COGNITIVE PLASTICITY: AGING AND GENETICS

Cognitive plasticity is the capacity to acquire or improve cognitive skills (e.g., the ability to solve problems or recall events). It varies across individuals, species, and throughout the lifespan, and can be influenced by health and training. For example, individual children (ages 9ï 10 years) vary dramatically with respect to the benefits they gain from practicing mnemonic strategies (Brehmer et al., 2007). Monkeys learn visual categorization tasks more slowly than do humans (Fig. 1a), suggesting that primates differ in their capacity to acquire this cognitive skill (Smith, Minda, & Washburn, 2004). Most adults can improve their memory recall by learning to use imagery-based memorization techniques (Fig. 1b), but elderly individuals often benefit less from such memory training than do younger adults (Baltes & Kliegl, 1992). Such differences in cognitive plasticity raise important questions about the cognitive and neural processes underlying intellectual abilities and the efficiency of general age-based educational strategies.

CORTICAL CONTRIBUTIONS TO COGNITIVE PLASTICITY

The neural mechanisms that determine an organismȏs capacity to acquire or improve cognitive skills remain unclear. It is almost universally accepted, however, that the cerebral cortex is essential to intellectual aptitude. Cortical function might increase cognitive plasticity by increasing working memory, selective attention, self-reflection, hierarchical association, the capacity for symbolic thought, observational learning, numerical competence, abstraction, consciousness, executive functions, and so on. Current explanations for how cortical processing gives rise to cognitive skills typically focus on specializations that enable humans to perform unique intellectual feats. In contrast, I proposed that cognitive plasticity reflects the precision and flexibility with which cortical networks differentiate event representations, and consequently that intellectual capacity is determined by basic structural, functional, and adaptive properties of cortical networks that constrain the cortical resolution of events (Mercado, 2008).

The structural foundation of my framework is the cortical module. Cortical modules are defined by neuroanatomists (e.g., Zaborszky, 2002) as compact cortical circuits that consist of vertical, interconnected columns of neurons. Unlike cognitive modules, which are hypothetical mental subroutines for performing specialized cognitive functions, cortical modules can be directly observed using both histological and electrophysiological techniques. Cortical modules vary structurally across different cortical regions. For example, Brodmannȏs areas describe topographical variations in cortical architecture; these variations reflect differences in the distribution of various types of neurons within cortical modules. Although the diversity of cortical modules is consistent with current proposals that cortical circuits are functionally specialized, how such diversity relates to particular functional capacities remains unknown. Furthermore, structural regularities apparent throughout cortical networks strongly suggest that, despite their differences, all cortical modules likely perform similar computations. Identifying how cortical modules contribute to cognitive plasticity is an important step toward explaining variations in this capacity as well as toward developing new ways of increasing intellectual capacity.

Availability of Cortical Modules

Structural neuroimaging studies show that the physical size of several brain regions is positively correlated with behavioral measures of intelligence (Jung & Haier, 2007). Researchers have also related cross-species differences in cortical structure to differences in behavioral flexibility (Healy & Rowe, 2007). Although the relationship between cortical size and cognitive capacity is far from one-to-one, on average more cortex seems to be linked to greater capacity. This correlation reveals little, however, about why additional cortex is advantageous for some individuals and species but not for others. The individual with a larger cortex may have more neurons, more synapses, bigger neurons, or more room for dendritesð any of these differences might confer advantages. I have proposed, however, that greater cortical volume is associated with higher cognitive plasticity because a more expansive cortex provides more space within which a larger quantity and greater diversity of cortical modules can be distributed (Mercado, 2008). Put another way, the absolute or relative size of cortex does not determine an organismôs capacity; capacity depends on the availability of cortical modules.

A novel prediction of my framework is that two individuals with equal cortical volumes can have radically different cognitive capacities, depending on how their modules are structured and distributed. Furthermore, this framework predicts that cross-species differences in behavioral flexibility are more closely related to differences in the number and diversity of cortical modules than they are to ratios between different types of brain tissue. A rat is much smaller than a cow, but they both have four limbs and thus can walk using similar strides. A ratôs limbs are diversified in ways that a cowôs are not, however, and consequently rats can manipulate objects more flexibly than cows can. Current evidence suggests that cognitive plasticity in rats is higher than it is in cows, even though rats have many less neurons and synapses than cows do. My framework predicts that detailed comparisons of cortical structure will reveal that rats possess a greater number and/or diversity of cortical modules.

Think of cortical modules as being like muscle fibers: Both are bits of tissue that are useless alone but functional in numbers. You can make reasonable predictions about the amount of force an organism can produce if you know how much its muscles weigh. More muscles correlate with greater strength. If, however, your goal is to predict what an organism can physically do (e.g., whether it can fly), then you need to know more about structural details such as the number, size, and spatial distribution of muscle fibers. Similarly, when it comes to predicting what an organism can mentally do, knowing the quantity and characteristics of its cortical modules is more useful than simply knowing the size of its cortex.

Coordinating Cortical Modules

Functional neuroimaging studies show that brain regions play different, predictable roles during different stages of cognitive-skill acquisition. Which cortical modules are involved in a particular stage of skill learning depends on the age and proficiency of the learner, the task being learned, and the strategies that the individual uses. Similar learning-related, regional shifts in cortical activity are seen in monkeys as they become proficient at performing visual classification tasks (Yokoyama, Tsukada, Watanabe, & Onoe, 2005). These findings suggest that cognitive plasticity reflects not only the availability of appropriate cortical modules but also the ability to dynamically select which modules are engaged during learning.

Circuits in the frontal lobes likely determine when cortical circuits are dynamically reconfigured (Sridharan, Levitin, & Menon, 2008). Structural and functional variability in frontal circuits is also associated with individual differences in intelligence (Jung & Haier, 2007), working-memory capacity (Westerberg & Klingberg, 2007), and the capacity to mentally switch gears (e.g., through cognitive control or executive functions). Collectively, these findings are consistent with the proposal that cortical reconfigurability contributes to intellectual capacity and suggest that the frontal cortex facilitates interactions between modules. Researchers must directly control cortical dynamics during experiments, however, to demonstrate that differences in reconfigurability influence an organismôs cognitive plasticity.

Returning to the muscle analogy, an individual must possess appropriate finger muscles to learn certain skills such as playing the piano, but that is not sufficient. The person must also be able to flexibly coordinate activity in those muscle fibers. An organismôs capacity to dynamically coordinate cortical modules may similarly determine which cognitive skills it can easily learn; increases in cortical dexterity should increase cognitive plasticity.

Plasticity of Cortical Modules

Santiago Ramón y Cajal suggested early on that learning generates improvements by dynamically changing cortical networks (Azmitia, 2007). Cajal was not talking about shifts in activity across cortical regions, however, but about changes in the physical connections between cortical neurons (a form of neural plasticity). Traditionally, intelligence researchers and cognitive scientists have downplayed the relevance of neural plasticity to understanding individual or species differences in cognitive capacity. In contrast, I proposed that cortical plasticity is a major determinant of cognitive plasticity (Mercado, 2008).

To say that cortical modules are plastic is simply to say that their form and function varies systematically throughout the lifespan as a result of their activity. Cortical modules naturally change with development in ways that depend on sensory experience. For example, in individuals born blind, modules in the visual cortex may become reorganized to process tactile or auditory inputs. Training with odors increases adultsô ability to distinguish them, and increases the selectivity with which cortical modules respond to different odors (Li, Howard, Parrish, & Gottfried, 2008). Structural changes in cortical modules also can be related to differences in cognitive capacity. For example, complex changes in the thickness of the frontal cortex during development are correlated with changes in IQ (Shaw et al., 2006). Cortical plasticity can affect the availability of particular kinds of modules, which may in turn affect an organismôs cognitive plasticity.

Many researchers assume that cortical regions that are relatively large in primates (i.e., the frontal lobes) determine intellectual capacity. In my framework, any neural system that contributes to cortical plasticity can potentially influence the capacity to improve cognitive skills (i.e., cognitive plasticity). In particular, subcortical regions that are present in all vertebrates can play a significant role in species and individual differences in intellectual capacity. For instance, neuromodulatory neurons near the brainstem that control activity levels throughout cortical networks (e.g., cholinergic neurons in the nucleus basalis) largely determine when auditory learning changes modules within the auditory cortex (Weinberger, 2004). Variations in neuromodulatory systems across species or individuals may thus contribute to differences in learning capacity. Interestingly, recent studies suggest that frontal circuits are highly interconnected with at least one of these subcortical neuromodulatory systems (Zaborszky, 2002), raising the possibility that frontal processing indirectly affects intellectual capacity by modulating the subcortical systems that control cortical plasticity.

As is the case with muscle fibers, the utility and flexibility of cortical modules depends in part on how they are used by the individual; in both cases, plasticity during development and training can increase capacity. The properties that determine how plastic a particular muscle fiber is, and the extent to which muscle plasticity can be controlled, are just beginning to be discovered. The factors that determine variability in cortical plasticity across species, ages, and individuals will need to be similarly characterized before the relationship between cortical plasticity and cognitive plasticity can be fully understood.

Summary

In the proposed framework, (a) the brainôs ability to differentiate events determines an organismôs capacity to learn cognitive skills; (b) small local networks of cortical neurons (cortical modules) vary structurally across cortical regions; (c) the diversity and quantity of cortical modules available determine the brainôs capacity to differentiate events; (d) only a subset of available modules are used to process an event; (e) frontal circuits coordinate the cortical modules engaged during event processing; (f) experience customizes modules; (g) module customization is controlled by subcortical neuromodulatory systems; and (h) frontal circuits can influence experience-dependent customization of modules (Fig. 2). Within this framework, cortical modules play a similar functional role to the ñcellsò in Hebbôs theory of cell assemblies. Namely, networks of modules develop over time, enabling an individual to perceive similarities and differences between events. These acquired perceptual representations subsequently facilitate development of the concepts necessary for an individual to learn or improve cognitive skills.

LINKS BETWEEN PERCEPTUAL CAPACITY AND COGNITIVE PLASTICITY

If cortical modules facilitate learning by increasing an individualôs ability to distinguish events, then variations in cognitive plasticity across ages, individuals, and species should be associated not only with differences in cortical structure and function but also with differences in an organismôs capacity to make perceptual distinctions. Consistent with this prediction, overall perceptual acuity correlates highly with IQ (Deary, Bell, Bell, Campbell, & Fazal, 2004), and childrensô ability to differentiate and act on spoken words is a good predictor of their future reading skills. Similarly, cognitive aging research has revealed parallel decreases in perceptual abilities and cognitive capacities. Such correlations suggest either that intellectual ability is a function of perceptual acuity or that some common mechanism underlies individual differences in both capacities. In my framework, both cognitive plasticity and perceptual resolution depend on the experience-dependent differentiation of events by cortical modules (i.e., both perceptual processing and cognitive-skill learning are constrained by the fidelity of cortical representations of events). Thus, the framework predicts that both perceptual acuity and common mechanisms underlying cortical plasticity and reconfigurability contribute to these correlations. Future studies that directly compare perceptual learning capacity, cognitive plasticity, and cortical differentiation of events within and across individuals can clarify the links between perceptual and intellectual capacities.

MONITORING AND MANIPULATING CORTICAL FUNCTION

Neuroimaging studies have revealed the dynamics and diversity of cortical regions involved in cognitive-skill learning and intelligence, but they have proven to be less useful for predicting an individualôs learning potential. New techniques for measuring details of cortical and subcortical circuitry and activity are needed to identify the sources of differences in capacity.

Additionally, new methods for controlling the structure or function of neural circuits, and for measuring the effects of such manipulations on cognitive plasticity, can provide important new insights about how experience modulates cortical processing (and vice versa). For example, cortical responses to acoustic events can be radically changed in adult rats (such that the area of cortex responsive to sound more than quadruples in size) by externally controlling electrical activity in subcortical neuromodulatory circuits during the presentation of sounds (Mercado, Bao, Orduña, Gluck, & Merzenich, 2001). The impacts of such extensive cortical changes on perception and learning are unknown. By combining neurophysiological techniques for modifying cortical processing with behavioral and neural measures of cognitive-skill learning, researchers can directly evaluate how the availability and selectivity of cortical modules affects perceptual acuity and cognitive plasticity.

ENHANCING COGNITION

Recent advances in rehabilitation science and athletic performance enhancement provide a glimpse into the future of cognitive plasticity studies. Physiologists have identified several properties of muscle fibers that determine their strength and plasticity. This knowledge has led to the development of more effective exercise programs for increasing muscle capacity, as well as to the development of pharmacological agents that amplify muscle plasticity. Consequently, professional athletes have increased their physical capacity far beyond that of previous generations and could achieve even higher levels were use of performance-enhancing substances not prohibited.

Are comparable techniques for increasing mental capacity feasible? Perceptual and cognitive training regimens that can improve auditory memory (Mahncke et al., 2006), working memory (Westerberg & Klingberg, 2007), language skills (Tallal, 2004), and even intelligence

(Jaeggi, Buschkuehl, Jonides, & Perrig, 2008) already exist. Similar training techniques have been used to forestall age-related cognitive decline and to mitigate the negative effects of attention deficit hyperactivity disorder. Increases in the size of cortical regions engaged during memory tasks accompany increases in an individualôs working-memory capacity (Westerberg & Klingberg, 2007). Undoubtedly, a clearer understanding of the neural mechanisms that determine cognitive plasticity will give rise to more powerful technologies for enhancing cognition, including new ways for teachers to tailor educational interventions to suit the particular needs of individual students.

Brain ñsteroidsò and cognitive training may sound like a godsend. Without a clear understanding of the mechanisms that engender cognitive plasticity, however, the potential for quackery and unforeseen negative side effects is great. Many college students already are taking Ritalin in a vain attempt to boost their grades. What will happen if drugs or other technologies that significantly enhance cognition become available? Will parents spend more time selecting the right drug cocktail for their child than on choosing the right school? Might dolphin cognition be enhanced to the point where dolphins stop answering questions and start asking them? New technologies for increasing cognitive plasticity have ethical implications far beyond those raised by doping in sports; the phrase ñchanging your mindò may soon take on a whole new meaning.

Recommended Reading

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Jones, S., Nyberg, L., Sandblom, J., Neely, A.S., Ingvar, M., Petersson, K.M., et al. (2006). Cognitive and neural plasticity in aging: General and task-specific limitations. *Neuroscience and Biobehavioral Reviews*, *30*, 864ï 871. A recent review of studies that examine age-related changes in the ability to learn or improve cognitive skills.

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Figure Captions

Fig. 1. A comparison of humansô(H) and monkeysô(M) performance (% correct) as they learned visual categorization tasks (a) and differences in the rate and level of improvement across old (O) and young (Y) age groups during memory training (b). Panel a adapted from ñCategory Learning in Rhesus Monkeys: A Study of the Shepard, Hovland, and Jenkins (1961) Tasks,ò by J.D. Smith, J.P. Minda, & D.A. Washburn, 2004, *Journal of Experimental Psychology: General*, *133*, pp. 398ï 414. Copyright 2004, American Psychological Association. Adapted with permission. Panel b adapted from ñFurther Testing of Limits of Cognitive Plasticity: Negative Age Differences in a Mnemonic Skill Are Robust,ò by P.B. Baltes & R. Kliegl, 1992, *Developmental Psychology*, *28*, 121ï 125. Copyright 1992, American Psychological Association. Adapted with permission.

Fig. 2. Schematic illustration of how cortical structure and function may constrain cognitive plasticity. Cortical modules vary in diversity and number across the cortical surface. Global neuromodulatory systems send projections throughout these modules. Neuromodulatory activity can affect the number of cortical modules engaged during cognitive-skill learning as well as during learning-related customization of modules. Prefrontal cortical networks respond to activity in other cortical modules and generate activity in global neuromodulatory systems,

thereby influencing the coordination of cortical modules as well as cortical reorganization. Collectively, these neural processes determine the resolution with which ongoing events are cortically represented, which in turn determines the rate and level of cognitive-skill learning. Adapted from ñNeural and Cognitive Plasticity: From Maps to Minds,ò by E. Mercado, III, 2008, *Psychological Bulletin*, *134*, 109ï 137. Copyright 2008, American Psychological Association. Adapted with permission.

Figure 1

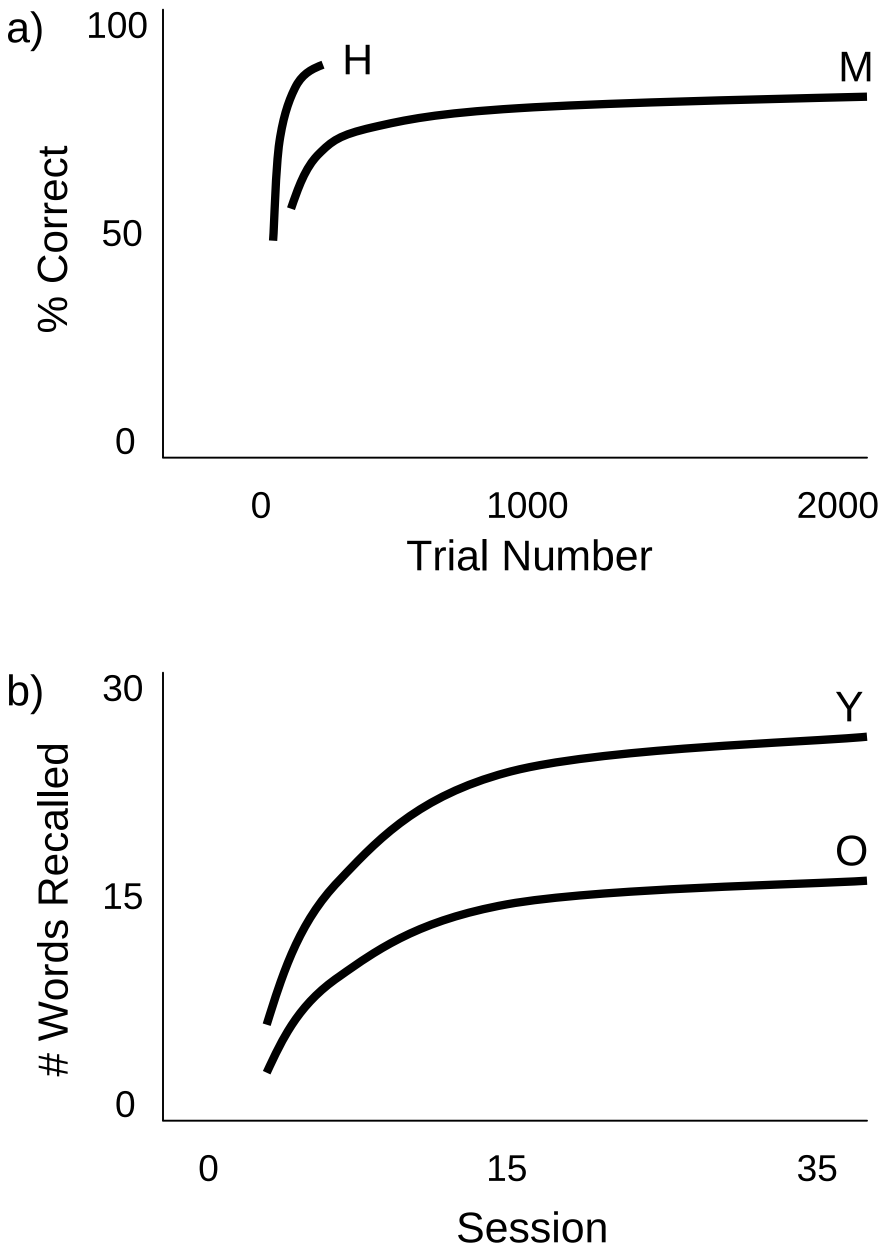
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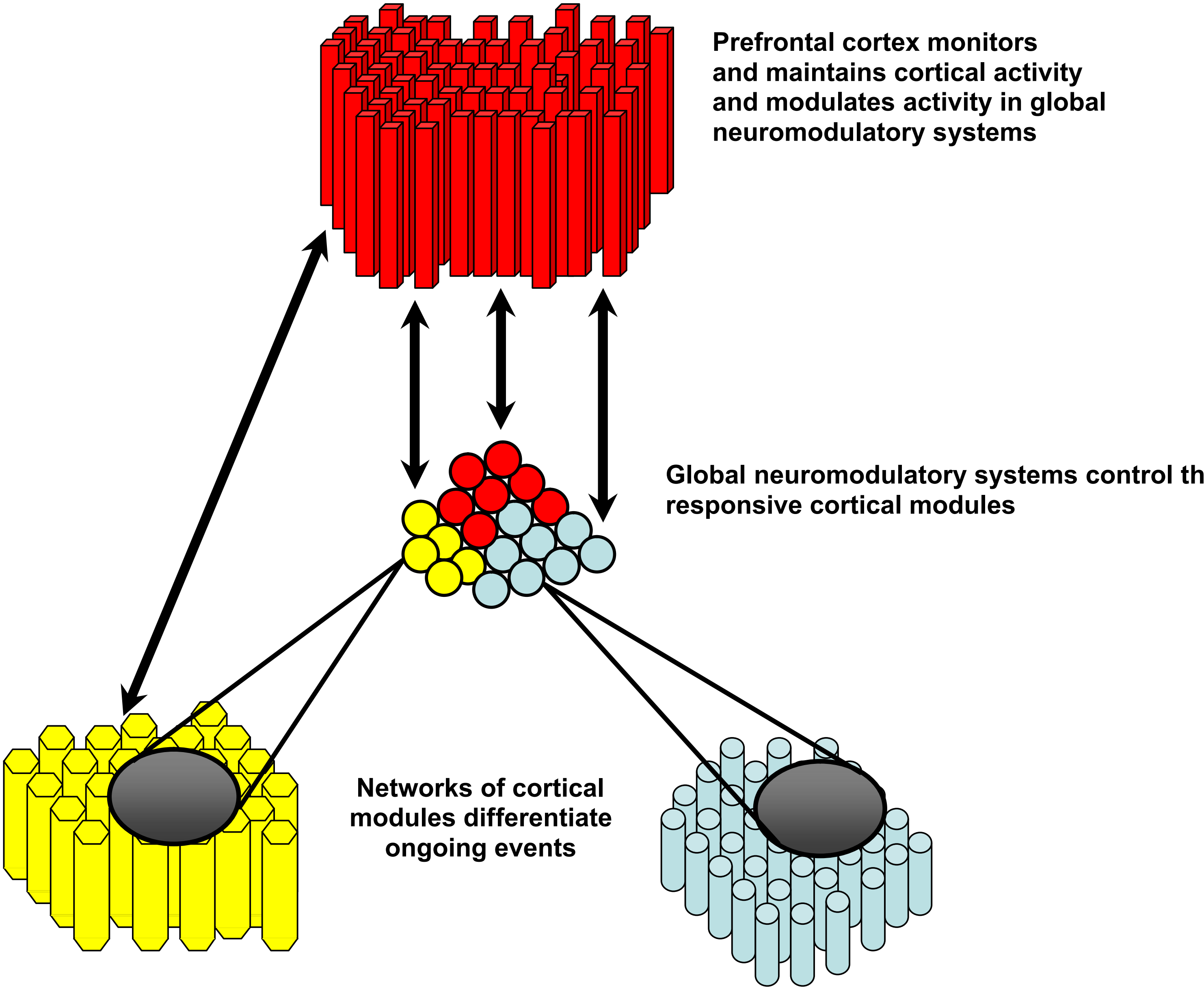
Figure 2


Prefrontal cortex monitors
and maintains cortical activity
and modulates activity in global
neuromodulatory systems
Global neuromodulatory systems control th
responsive cortical modules
Networks of cortical
modules differentiate
ongoing events