# Decentering Cognition

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## Abstract

The neocortex figures importantly in human cognition, but it is not the primary locus of cognition or even at the top of a hierarchy of cognitive processing areas in the central nervous system. Moreover, the form of information processing employed in the neocortex is not representative of information processing elsewhere in the nervous system. In this paper, we articulate and argue against cortico-centrism in cognitive science, contending instead that the nervous system constitutes a heterarchical network of diverse types of information processing systems. To press this perspective, we examine neural information processing in both non-vertebrates and vertebrates, including examples of cognitive processing in the vertebrate hypothalamus and basal ganglia.

**Keywords:** cortico-centric perspectives; heterarchical organization; neuromodulators; neuropeptides; hormones; hypothalamus; basal ganglia

## 1. Introduction

The neocortex is often viewed as the locus of cognitive activities in the brain. To many cognitive scientists, this cortico-centric view of cognition seems just obvious. The cortex is the locus to which the senses project information and from which motor commands originate. Cognition is what occurs between these inputs and outputs as information is processed through a sequence of cortical areas until decisions are made in executive regions in the prefrontal cortex and commands issued to motor regions of cortex. (In recent years, some cognitive theorists have expanded their focus beyond the neocortex to include the loops linking cortex with the thalamus and basal ganglia. Even for these theorists, the cortex is central.) We call this view *cortico-centrism* and distinguish two focal components: the mode of *synaptic transmission* and *hierarchical structure.*

Signals are transmitted between cortical neurons primarily through neurotransmitters such as GABA and glutamate. What is characteristic of neurotransmitters is that they operate within a synapse: they are transported, typically in small vesicles, to the presynaptic terminal from which they are released into the synaptic cleft. Some molecules bind to receptors on the postsynaptic neuron, but those that do not are quickly removed from the synaptic cleft. As a result, synaptic information transmission tends to be highly specific on temporal and spatial scales. However, outside neocortex, many neurons communicate with what are called *volume transmitters* (dopamine, serotonin, histamine, etc.) or neuropeptides (small molecules released from nerve cells which mostly act on G-protein coupled receptors). These are often released in large vesicles at locations other than synapses, including in the cell body. They are not broken down at the site but diffuse through cerebral spinal fluid or the circulatory system and affect the activity of many neurons or other cells that have receptors to which they can bind. Thus, information transmitted through volume transmitters and neuropeptides is much less specific on both temporal and spatial scales. These molecules often bind to neurons that also communicate using traditional neurotransmitters. Because they modify the excitability, synaptic efficiency, and dynamics of neurons and alter the cognitive processing of the circuit in which the neuron is situated, they are characterized as neuromodulators. Thus, the first focus of cortico-centrism, synaptic transmission, refers to the tendency to overemphasize the roles of neurotransmitters over volume transmitters and neuropeptides in information processing.

The second focus, hierarchical structure, limits one's focus to one type of cognitive architecture as responsible for processing information, one in which a small number of cell types are organized into a stereotypic architecture of columns and connections between them. Moreover, the connections between brain regions are predominantly conceptualized as from the lower-sensory areas to the higher, central "cognitive" areas, and then down to the motor areas. (In recent years, researchers have recognized the bidirectional flow of information as well as the direct connections between sensory and motor areas, but still accommodate these extensions within the hierarchical picture.) To a reasonable approximation, the focus on hierarchical structure fits the neocortex. However, it does not characterize other brain regions that consist of nuclei of neurons that reside in distributed networks in which they integrate inputs from and transmit outputs to a broad range of other nuclei.

Both synaptic transmission and hierarchical structure are illustrated in many artificial neural networks. Networks are hierarchical as inputs are processed through a sequence of layers until outputs are generated. The connections between nodes reflect synaptic transmission—it is often the only kind of information flow they model. Finally, we note that the second focus is also strengthened by the first one: by foregrounding connections based on neurotransmitters (and backgrounding all others), the hierarchical structure in the cortex seems much more compelling.

To show the limits of cortico-centrism, we adopt a phylogenetic perspective. Perceiving, categorizing, decision making, coordinating motor responses etc., are activities all organisms must perform to maintain themselves as organized systems far from equilibrium with their surroundings, a

condition that requires them to procure energy and material resources while avoiding destructive forces in their environments (Moreno & Mossio, 2014). A phylogenetic perspective reveals how multiple, partly independent information processing activities developed, taking advantage of chemical processing. Although these activities are important for prokaryotes, plants, fungi, and animals lacking neurons,[1] we limit our focus here to animals with neurons. We begin in section 2 with Cnidarians, and in section 3 consider an invertebrate—*C. elegans*. In sections 4 and 5 we turn to vertebrates, focusing on two structures outside of cortex found in all vertebrates that perform important cognitive functions—the hypothalamus and the basal ganglia. We conclude by considering the implications of a decentered perspective on the brain for cognitive science.

## 2. Decentered Cognition in Cnidarians

Cnidarians (jellyfish and polyps) branched off from other animal species very early[2] and provide a glimpse into one of the earliest nervous systems. The core part of the nervous system in Cnidarians is a nerve net that lies between two layers of cells—epidermis and gastrodermis—that constitute the bell. The nerve net includes what have been identified as sensory and motor neurons that together coordinate the behavior of contractile epidermal cells (Keijzer, van Duijn, & Lyon, 2013). The nerves whose processes cross each other in the nerve net communicate bidirectionally by releasing neuropeptides that gate ion channels in the other neuron (Golubovic et al., 2007; Grunder & Assmann, 2015).

The nerve net provides an information processing backbone, but processing in the nerve net is altered by other neurons that project onto it. There are two rings of neurons surrounding the bell. Neurons in the inner ring serve as pacemakers, creating a rhythmic pattern of contraction of the bell during swimming. But signaling from elsewhere in the organism serves to stop the pacemaker and hence swimming when, for example, a threat is detected or the jellyfish is eating. Often this information is conveyed chemically, leading Bosch et al. (2017) to claim "that the cnidarian nerve net, while structurally simple, is chemically complex" and to propose that it might rely on a "chemical connectome" in which it is not the specific set of synapses that determines activity, but the distinctive receptors that respond to transmitter substances that are distributed widely.

In short, Cnidarian nervous systems illustrate that the features we associate with cortico-centrism are not universal. Cnidarians neither exhibit hierarchical structure nor rely exclusively on synaptic transmission for producing adaptive behaviors.

## 3. Decentered Cognition in Invertebrates

Invertebrate nervous systems also violate these features of cortico-centrism. As the first organism for which researchers generated a nearly complete connectome (White, 1985; White, Southgate, Thomson, & Brenner, 1986; for a more recent update, see Varshney, Chen, Paniagua, Hall, & Chklovskii, 2011), *C. elegans* has provided a model organism for determining circuits involved in different behaviors. Indeed, in conjunction with the research on the connectome, Chalfie et al. (1985) characterized a circuit controlling backwards and forwards locomotion in response to a light touch to the head or tail (Figure 1). The sensory neuron for posterior touch, PLM, is connected by both chemical synapses and gap junctions (which connect the cytoplasm of two cells directly) to PVC, which sends excitatory connections to the motor neurons required for accelerating forward motion. In a similar way, anterior touch results in reversal and backward movement. This circuit became the model of other networks involved in chemotaxis, foraging, feeding, egg-laying, etc. in *C. elegans*, with different circuits for each activity.
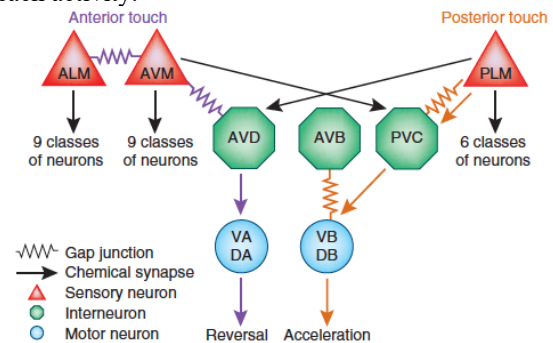


Figure 1. Circuit controlling forwards (Acceleration) and backward (Reversal) locomotion in *C. elegans.* From (Bargmann & Marder, 2013).

The identification of distinct circuits for different activities in *C. elegans* already reveals a highly decentered, heterarchical cognitive system[3] in which distinct neural mechanisms process and utilize information for each of the worm's activities. The individual circuits still appeared hierarchical; however, subsequent studies on the mechanisms represented in Figure 1 pointed to a more complex network of interneurons and ways in which volume transmitters and neuromodulators modify the behavior of the circuit. For example, while a diverse set of sensory neurons could initiate an avoidance response to the repulsive odor of octanol when the worm was starved, only one neuron could do so when it was well-fed. This change could be induced by the application of exogenous serotonin, known to be associated

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[1] *Trichoplax adhaerens* provides a useful model of an animal without neurons. It has most of the components that in subsequent evolution were packaged into neurons, including a number of peptides. It has only six types of cells, whose activities are coordinated. Senatore, Reese, and Smith (2017) identified endomorphin-like peptides released by sensory cilia that function to arrest beating of motor cilia during feeding. The endomorphin-like peptides also facilitate communication between organisms.

[2] There is a debate as to whether Ctenophora branched earlier, perhaps even before Porifera (Kristan, 2016).

[3] The notion of heterarchy was introduced by McCulloch (1945) for non-hierarchical relations between values, but it is used here to describe systems that are not organized hierarchically—in which outputs from one component are distributed to many other components and there is no pyramid in which one or a few units constitute the highest processing level.

with food-related behaviors (Chao, Komatsu, Fukuto, Dionne, & Hart, 2004). Subsequent research revealed that other amines—dopamine, tyramine, octopamine—as well as neuropeptides, released by a variety of different neurons, could also modulate the activity of the network (Wragg et al., 2007; Mills et al., 2012). Bargmann (2012) concludes from these and other findings that "information flow through *C. elegans* circuits depends on neuromodulatory states." (p. 461).

## 4. Decentered Cognition in Vertebrates: The Hypothalamus

A major feature of phylogenetic development in the evolution of bilaterally symmetric organisms is the centralization of neural ganglia in the anterior of the organism, creating a brain. Invertebrate brains are often contrasted with vertebrate brains, where the later, equipped with cerebral cortex (or pallium), are viewed as far more integrated, whereas the invertebrate brain is simply a collection of ganglia, each with different functions (Zullo & Hochner, 2011). As a result, one may argue that cortico-centrism naturally applies to only animals with a neocortex, i.e., to vertebrates. In this section and the next, we offer evidence that this difference is exaggerated—the vertebrate brains also contain multiple distinct processing areas and violate the two features of cortico-centrism.

An important finding in recent years is that the basic plan of the vertebrate brain is highly conserved. Regions have expanded differentially; in particular, the small pallium of the first vertebrates has expanded into the massive neocortex of humans. But structures such as the hypothalamus, basal ganglia, thalamus, and cerebellum were all present in the common ancestor of vertebrates (Grillner & Robertson, 2016). These and other structures play important roles in cortical information processing, but they are also adequate to generate much of the ordinary behavior of animals without the neocortex, as revealed by research on decorticate animals (primarily cats) in the second half of the 20th century (Bjursten, Norrsell, & Norrsell, 1976).

We start with the hypothalamus, which processes information important for many behaviors but is organized in a radically different manner than the neocortex. Rather than following the two features of synaptic transmission and hierarchical structure, the hypothalamus achieved its specialized functions through "hundreds, perhaps thousands of chemically, connectionally, and functionally distinct cell populations" (Saper & Lowell, 2014). These different populations respond to different information about the state of the organism and send out regulatory signals that modulate physiological and motor systems, and other neural systems.

To illustrate the type of regulation performed by the different nuclei of the hypothalamus, we focus on just one example, the regulation of arousal by the hypocretin/orexin system. When hypocretin neurons were first identified (de Lecea et al., 1998; Sakurai et al., 1998), they were characterized as promoting feeding behavior. A variety of studies soon pointed to their role in arousal as well.

Recording from these neurons revealed that they fired maximally 10-20 seconds prior to a sleep-to-wake transition (Lee, Hassani, & Jones, 2005), while optogenetic activation promoted wakefulness (Adamantidis, Zhang, Aravanis, Deisseroth, & de Lecea, 2007). Silencing these neurons, in contrast, induced slow-wave sleep (Tsunematsu et al., 2013).

An important feature of these neurons is that they project to and release hypocretin in a large number of brain regions which have also been implicated in arousal (figure 2). For example, they project to the locus coeruleus where experimental administration of hypocretin promotes arousal (Gompf & Aston-Jones, 2008) while silencing hypocretin release prevents sleep-to-wake transitions. (The locus coeruleus, in turn, is a primary source of cortical noradrenaline—a neuromodulator involved in regulating wakefulness, among other functions.) Other loci to which hypocretin neurons project are the dorsal raphe nuclei and the ventral periaqueductal gray, which contain serotonin and dopamine neurons whose activations generate the rapid transition from sleep to wakefulness (Moriya et al., 2017; Cho et al., 2017). Another dopaminergic center to which the hypocretin cells project is the ventral tegmental area (VTA). Although not traditionally linked to arousal, dopamine neurons in the VTA have now been implicated in wakefulness (Eban-Rothschild, Rothschild, Giardino, Jones, & de Lecea, 2016).
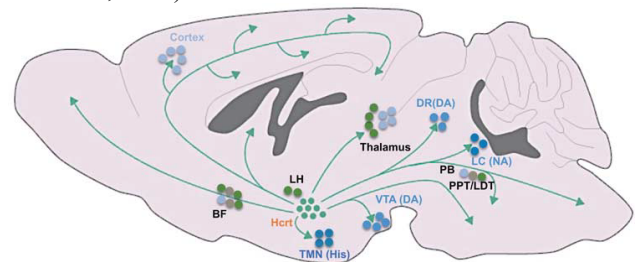


Figure 2 Projections in the rat brain from hypocretin neurons in the thalamus. Figure from Eban-Rothschild, Appelbaum, and de Lecea (2018).

We return to the VTA below, but to flesh out the picture of how hypocretin neurons process information, it is important to realize that they not only project broadly but receive input from multiple locations. Using retrograde tracers, Yoshida, McCormack, Espana, Crocker, and Scammell (2006) identified projections into regions containing hypocretin neurons from allocortex, claustrum, lateral septum, bed nucleus of the stria terminalis, many hypothalamic regions (e.g., the preoptic area, dorsomedial nucleus, lateral hypothalamus, posterior hypothalamus), as well as various brainstem regions (e.g., the periaqueductal gray matter, dorsal raphe nucleus, and lateral parabrachial nucleus). Inputs from the amygdala and bed nucleus of the stria terminali to the hypocretin neurons suggest how emotional states can affect the sleep-wake cycle. Inputs from the suprachiasmatic nucleus, primarily relayed via the subparaventricular zone and dorsomedial nucleus, are of particular significance since they carry information about circadian time.

A variety of hormones also affect the activity of hypocretin neurons. Leptin, which is secreted by adipocytes and correlates with satiety, inhibits hypocretin neurons. When leptin levels are reduced during fasting, hypocretin neurons increase activity and promote wakefulness (Leinninger et al., 2011). Likewise, ghrelin increases during fasting and also generates increased hypocretin activity. Relatedly, ghrelin itself generates feeding, but this can be blocked by attenuating hypocretin signaling (So et al., 2018). As a final example, there is a positive feedback loop between stress and hypocretin activity: stress activates hypocretin neurons (Winsky-Sommerer, Boutrel, & de Lecea, 2005), while hypocretin activity, in turn, results in subsequent increase in circulating glucocorticoids (Bonnavion, Jackson, Carter, & de Lecea, 2015).

The picture that emerges is that hypocretin neurons regulate other brain and behavioral centers based on integrating information carried by a rich array of volume transmitters and neurotransmitters from a variety of sources relevant to the need for arousal. Hypocretin neurons are just one example of hypothalamic neurons that process information and regulate behavior in ways that defy the design principles of cortico-centrism.

## 5. Decentered Cognition in Vertebrates: The Basal Ganglia

One may object that most of the behaviors regulated by the hypothalamus are not particularly "cognitive" and that it is cognitive behaviors, such as deliberate decisions, that are distinctively human and subject to the design principles of cortico-centrism. We shall argue that cortico-centrism is false even for high-level cognition by turning to our second example of non-cortical mechanisms in the vertebrate brain, the basal ganglia. The basal ganglia are a connected set of subcortical nuclei that have been identified as playing important roles in a variety of functions, such as sensorimotor processing, motivated behavior, reward learning, and "cognitive" activities of working memory, model-based planning, and attention.

One distinctive feature of the basal ganglia is that they cannot be situated within the cortical hierarchy because they receive inputs from and send outputs to an extraordinary number of other brain regions, including sensorimotor, associative, and motivational areas of the cortex, but also non-cortical areas such as motor command regions in the midbrain (Figure 3). Another feature is that the basal ganglia exhibit a *heterarchical* internal organization that enables them to play crucial roles in the selection of internal and external responses. Here, we present a simplified picture to illustrate how the organization serves this function (Figure 4). Different neurons in the input nuclei, known collectively as the striatum, project along one of two pathways to the output nuclei, the substantia nigra pars reticulata and the globus pallidus internus. The default activity of the output nuclei is to inhibit other brain regions, typically those from which the input originated. Projections along what is known as the direct pathway serve to reduce this inhibition, allowing these

other brain regions to carry out their activity, while projections along the indirect pathway serve to enhance the inhibition to these regions. However, the two pathways interact with other nuclei in the basal ganglia to make selections. For example, the hyperdirect pathway intervenes to reduce impulsive and suboptimal decisions. By determining which areas are released from tonic inhibition, the basal ganglia select internal and external responses, including working memory updates, attentional shifts, as well as motor behaviors.

It is particularly salient that the basal ganglia and thalamus can execute their various activities in behavior coordination even in decorticated animals. Whether working with cortex or other brain regions, the basal ganglia represent a different type of cognitive mechanism than found in the cortex.
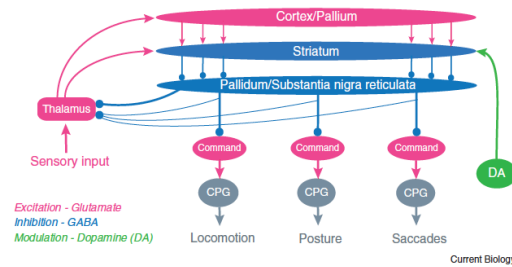


Figure 3. Common organization of inputs into and outputs form the striatum (shown in blue) in vertebrate brains. Figure from Grillner and Robertson (2016).
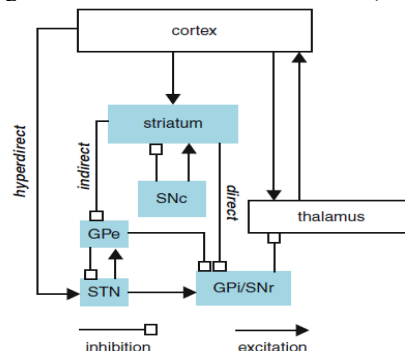


Figure 4. Major structures and pathways of the basal ganglia. Figure from Rubin (2015).

We have focused only on the role of the basal ganglia in response selection, but other cognitive activities such as reward learning, habit formation, and sequence learning have been attributed to it. In a particular striking example, Redgrave et al. (2010) provide evidence that competition between inputs from associative areas of cortex and prefrontal cortex is involved in switching from automatic, habitual processing to controlled, goal-directed processing.

Moreover, volume transmitters are essential for implementing the relevant information processing. An important input to the striatum, shown as DA in Figure 3, is provided by dopaminergic neurons in the VTA and the substantia nigra pars compactus. Dopamine, like other volume transmitters, disperses broadly from the cells that synthesize it and, by binding to receptors on other neurons, acts as a modulator on their activity. Dopamine signaling in the basal ganglia plays a variety of different roles, including

as a reward signal in reinforcement learning. Reduced dopamine in Parkinson's patients contributes to their inability to initiate actions and other more cognitive disabilities. Moreover, striatal neurons projecting into the direct and indirect pathways have different dopamine receptors, leading them to respond differently to dopamine release. A higher-level of tonic dopamine up-regulates the striatal neurons in the direct pathway while down-regulating those in the indirect pathway.

Adopting a comparative perspective, Hills (2006) advanced the hypothesis that dopamine plays a role in regulating explorative vs. exploitive behaviors in multiple domains. We noted in section 3 that in *C. elegans* dopamine acts as a modulator in the circuit for forward and backward movement. Hills, Brockie, and Maricq (2004) further showed that dopamine release in *C. elegans* leads to more turning, hence more investigation of the local area (exploitive behavior). Administration of a dopamine agonist, or ablation of the dopaminergic neurons, stops local search and results in the worm moving on to other locations (explorative behavior). Drawing upon this suggested role in regulating search in physical space, Hills et al. (2015) argue for the role of dopamine in regulating search in more cognitive domains such as memory and problem solving. While they do not emphasize it, the action of dopamine on the basal ganglia is the likely locus of these decisions about search across different domains.

Although our discussion is deliberately simplified, it reveals how the distinctive architecture of the basal ganglia allows for information processing different from that afforded by the cerebral cortex, but crucial for high-level cognition.

## Implications of Decentering the Brain

We have advanced examples from both non-vertebrates and vertebrates that reveal neural information processing very different from that performed in the neocortex. Unlike neocortex, much of this processing involves peptidergic and volume transmitters that behave differently than classical neural transmitters. Moreover, it occurs in heterarchically-structured networks. We have focused on just two examples of structures in vertebrate brains that differ from cortex in these respects and play important roles in determining behavior, but there are numerous others such as the superior colliculus, cerebellum and the thalamus that could be used to further illustrate our thesis. The upshot is that the vertebrate brain contains a large variety of neural processing systems that cannot be characterized by cortico-centrism.

The implications for cognitive science are two-fold. First, there are many other activities in the brain that are involved in processing information and regulating behavior. Many of these are commonly characterized in cognitive vocabulary and are performed independently of the neocortex. Rather than focusing on one central cognitive system, cognitive scientists should recognize that there are numerous different systems that each carry out specialized information processing tasks. Second, these systems employ architectures for processing information quite different from that provided by the cortex. Employing an artificial neural network for all tasks may lead to misrepresenting how the brain performs cognitive activities. This is not to deny the significance of neocortical processing, but to contextualize it within a larger cognitive system so as to recognize its distinctive contributions within that system while also recognizing that information processing in neocortex represents only one form of information processing important for cognition.

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