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Rethinking cognitive architecture: A heterarchical network of different types of information processors

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Abstract Rather than seeking a common architecture for cognitive processing, this paper argues that we should recognize that the brain employs multiple information processing structures. Many of these are manifest in brain areas outside the neocortex such as the hypothalamus, brain stem pattern generators, the basal ganglia, and various nuclei releasing neuromodulators. Rather than employing one mode of information processing, the brain employs multiple modes integrated in a heterarchical network. These in turn affect processing within the neocortex and together with the neocortex regulate vertebrate behavior, including human. Cognitive science can better understand human information processing by attending to the plurality of information-processing architectures employed in the brain.

KEYWORDS: Basal Ganglia; Cognitive Architectures; Heterarchical Networks; Hypothalamus; Pattern Generators; Neuromodulators

Riassunto *Ripensare l'architettura cognitiva: una rete eterarchica di differenti tipi di elaborazione di informazione* - Anziché cercare un'architettura comune ai processi cognitivi, in questo lavoro si sosterrà che dovremmo riconoscere come il cervello impieghi molteplici strutture per processare l'informazione. Molte di loro si trovano nelle aree cerebrali esterne alla neocorteccia, come l'ipotalamo, i generatori di pattern del tronco encefalico, i gangli basali e i vari nuclei che rilasciano i neuromodulatori. Anziché impiegare un'unica modalità per l'elaborazione dell'informazione, il cervello usa molteplici modalità integrate in una rete eterarchica. Queste, a loro volta, influenzano i processi all'interno della neocorteccia e, assieme alla neocorteccia, regolano il comportamento dei vertebrati, compreso quello umano. La scienza cognitiva può meglio comprendere l'elaborazione dell'informazione da parte degli esseri umani concentrandosi sulla pluralità delle architetture impiegate nel cervello per realizzare questa elaborazione.

PAROLE CHIAVE: Gangli basali; Architetture cognitive; Reti eterarchiche; Ipotalamo; Generatori di pattern; Neuromodulatori

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1 Introduction

Cognitive architectures have been developed in cognitive science to characterize the basic modes of processing information used in cognitive activities. These have, in general, featured a homogeneous set of capacities. Newell's SOAR architecture, for example, is a production system architecture in which matching items in working memory to the antecedents of rules results in changing the items in working memory.[1] Anderson's ACT employs a broader range of operations, but like SOAR treats cognitive activities as involving the application of rules to symbolically represented information. Developers of neural network architectures[2] broke with symbolic architectures by drawing inspiration from the brain. With the development of deep learning allowing for networks with many layers, investigators have developed network models of visual processing that map onto regions in the neocortex.[3] While the brain provided the inspiration for neural network architectures, only one part of the brain, the neocortex, was modeled. The neocortex is not representative of the rest of the brain. Moreover, it does not function on its own but is highly integrated with processing in other brain regions, especially the thalamus and the basal ganglia, which are in turn highly integrated with areas of the brainstem and midbrain. I will argue that in characterizing cognitive architectures, one should look more broadly in the brain. When one does so, one finds a heterarchical network of components implementing different information-processing architectures. The operation of the neocortex is integrated into the larger heterarchical network. My goal in this paper is to make the case that attention to these architectures and how they interact in the control of behavior can provide a more adequate grounding for cognitive science.

In arguing for a heterarchical network of different cognitive architectures, I embrace a perspective defended by Maturana and Varela,[4] among others, that all living organisms engage in cognition to regulate the activities through which they construct, maintain, and repair themselves. These activities must be regulated so that they are employed when and in the manner needed to maintain the organism as an autonomous system.[5] Recently a number of investigators have identified and sought to characterize cognitive processes in prokaryotes, plants, and invertebrates.[6] This is providing important new insights into how organisms process information. In this paper, however, I will limit my focus to vertebrates, and the role of the central nervous system in regulating the activities of vertebrates. Through extensive research comparing the human brain with that of the lamprey, a phylogenetic far distant vertebrate, Grillner[7] has argued that, except for the cerebral cortex, all vertebrate brains exhibit the same set of neural components organized in much the same manner. These include the diverse subcortical areas on which I will focus.

Although lacking a cerebral cortex (the neocortex plus structures such as the hippocampus), the lamprey does have a small pallium, a structure from which the structures in the cerebral cortex evolved. The pallium is, however, a relatively minor structure in the lamprey. Without cortical areas, the brains of lamprey, and presumably the earliest vertebrates, are able to process the information needed to perform the activities required to live. These activities include behaviors in an animal's environment, such as eating and defending itself. Moreover, research on decorticate preparations has shown that even mammals such as cats can, at least in the protected environment of the laboratory, conduct their lives without a cortex.[8] Their activities include, among others, the basic cognitive activity of making decisions about which actions to perform in different situations.[9] My focus will be on the different resources provided by some of the subcortical areas present in all vertebrates and preserved in decorticated mammals. With an appreciation of the type of information processing provided by these brain regions, I return in the section 6 to the neocortex and advance a perspective that its architecture, like that of the tectum that performs many of the same functions in early vertebrates, underlies a distinctive type of information processing that does contribute in important ways to the cognitive life of organisms that possess it. However, the neocortex is not a monolith, and individual regions of the neocortex are highly integrated with other brain regions that in many respects direct and regulate processing within it.

I cannot, in a short paper, present a comprehensive account of the different types of information processing architectures found in the vertebrate brain. Rather, I offer a brief introduction to five types of subcortical processing that together provide a perspective on the diversity of information-processing architectures on which vertebrates rely. I begin with the hypothalamus, whose nuclei serve to assess the needs of the organism (section 2), and central pattern generators and locomotor centers, that serve to coordinate muscle activity (section 3). The motor system is capable of generating many actions and some means of selecting which action to perform at a given time is required. This selection is performed by the basal ganglia, to which I turn in section 4.

Processing in the basal ganglia is influenced by dopamine. As I discuss in section 5, dopamine as well as other monoamines, such as serotonin and acetylcholine, are referred to as neuromodulators since they alter processing in neural circuits. I will argue that the nuclei that release these neuromodulators might better be seen as setting agendas for processing information. Many accounts of cognition treat it as processing sensory information, but none of the brain regions discussed so far processes sensory inputs. However, that is clearly required for effective motor activity. Although areas in the neocortex are viewed as principal areas for sensory processing, early vertebrates and decorticated animals rely on the tectum (also known as the superior colliculus). In section 6 I will briefly characterize information processing in the tectum and how the neocortex elaborates on its mode of processing. Processing sensory inputs, on the perspective I am advancing, is only one relatively specialized type of information processing underlying cognition, one that is used by other centers engaged in different modes of information processing.

The neural systems I discuss in sections 2-6 process information in diverse ways, each useful in enabling organisms to function in the world. To make sense of these diverse means of processing information, I return in the final section to how these modes of information processing serve the needs of an organism. An analysis of the brain that starts with the hypothalamus and brainstem systems of motor control focuses attention not on high-level abstract reasoning, but on directing activity needed for an organism to maintain itself. I also briefly consider the question of how the processing in these diverse areas, relying on different architectures, is coordinated to serve the organism. I challenge the widespread view that control systems such as the brain must be organized hierarchically, with the neocortex, and especially prefrontal regions of the neocortex, in charge. Instead, I argue that components with different cognitive architectures form a heterarchical network and together provide a robust stem for directing the activities of vertebrates.

One might object that the information processing in areas other than the cerebral cortex, while important for life, is not *cognitive* information processing. Debating the use of terms is generally not productive. One could restrict the term to conceptual reasoning,[10] solving problems,[11] or pattern recognition.[12] This, however, creates an unnatural division between domains of information processing, treating more traditionally cognitive activities as occurring autonomously from other information processing in the brain. It is noteworthy that much high-level human reasoning takes place in the context of recognized needs of the organism and is coordinated with action. Food is never far from people's minds, even when engaged high-level intellectual activities such as participating in academic conferences. Moreover, as I have already noted, neural activity in the cerebral cortex is integrated with that in the thalamus, and via the thalamus, with that of the brainstem and midbrain. The architecture in regions of the cerebral cortex is distinctive, but the information processing it carries out is integrated with that of the rest of the brain. I will revisit this theme after first describing the type of information processing used in other brain regions.

2 The hypothalamus: Assessing the needs of the organism

If organisms are to maintain themselves as systems far-from-equilibrium with their environments, they need to perform actions appropriate to their current condition. This means that they must procure information about their condition: Do they have sufficient nutrients? Are they confronting specific stressors? These assessments are made by nuclei in the brainstem (e.g., the nucleus of the solitary tract) and, in many cases, further processed in the hypothalamus. The hypothalamus comprises several small nuclei located adjacent to the median eminence at the base of the diencephalon. This is one of the few places in the brain without a blood-brain barrier.

The lack of a blood-brain barrier is important as the nuclei of the hypothalamus extend the information processing already performed in the endocrine system. The endocrine system relies on sensors that release chemicals that are transported through the blood stream to locations where they bind receptors and trigger biochemical activity. For example, in contexts in which ATP levels are low, indicating low reserves of energy and the need to procure more energy, the sight or smell of food or the digestion of it elicits insulin secretion from pancreas β cells into the bloodstream. Various other cells have insulin receptors and, when activated, initiate related activities.[13] For example, when liver cells detect insulin, they store glucose they don't need immediately as glycogen (without insulin, they extract glucose from glycogen and release it into the bloodstream). Insulin also promotes glucose uptake in adipose tissue where it is metabolized for fatty acid synthesis. Through these various responses, the organism directs the glucose it is acquiring but doesn't need immediately to replenishing energy reserves.

The fenestrated capillaries of the median eminence allow hormones in the blood to affect and be affected by neurons in the nuclei of the hypothalamus. Polypeptides comparable to those circulating in the blood provide a major currency for transmission between hypothalamic neurons. Polypeptides synthesized by neurons are referred to as *neuropeptides*. When neurons secrete a neuropeptide, it disseminates widely through the extracellular matrix. These neuropeptides can then bind to other neurons that have appropriate G-protein coupled receptors (GPCRs). Unlike ionotropic receptors, which respond by directly opening or closing ion channels, these receptors are

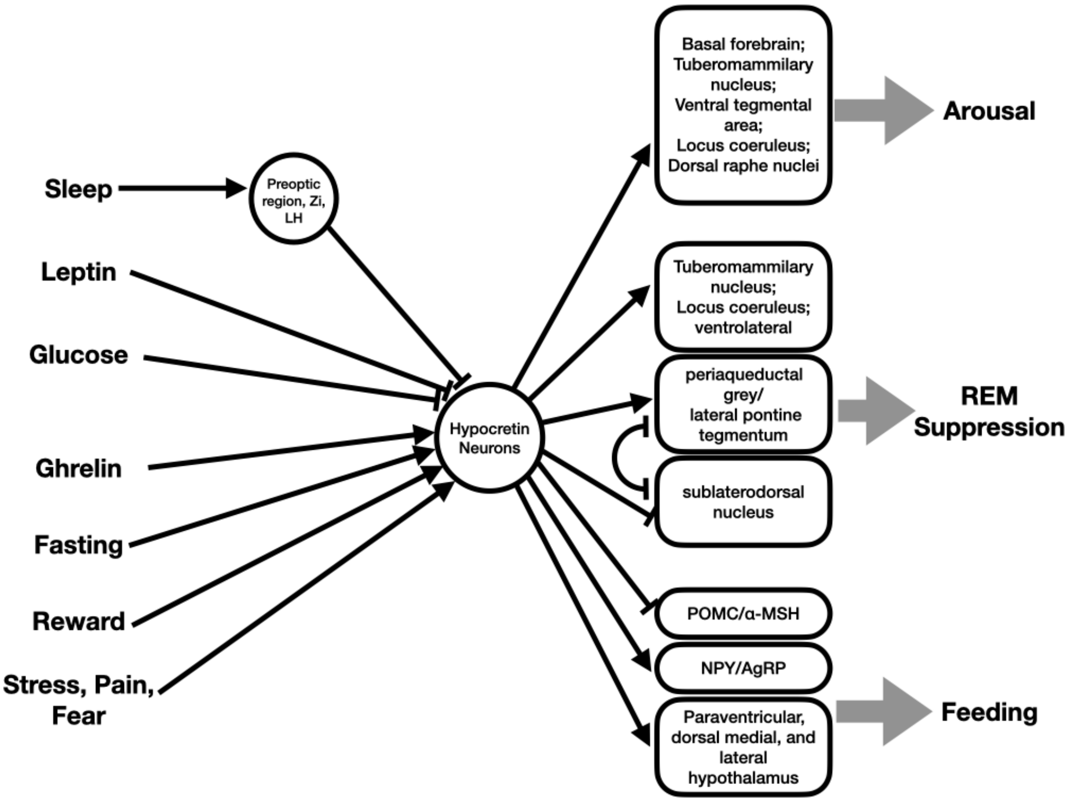

Figure 1. Inputs and outputs of hypocretin neurons, based on data reported by E. ARRIGONI, M.J.S. CHEE, P.M. FULLER, *To eat or to sleep: That is a lateral hypothalamic question*.

metabotropic: when appropriate ligands bind, they initiate intracellular signaling employing second messengers to initiate various metabolic activities, including the expression of targeted genes. The information processing in which these neurons engage is comparable to the chemical information processing in the endocrine system, with the difference that electrical transmission along axons and dendrites also enables delivering neuropeptides as well as more traditional neurotransmitters to neurons at distal locations.

Some hypothalamic nuclei contain cell populations that appear to respond to specific conditions in the body. The arcuate nucleus, for example, contains neurons that respond to different nutrient needs. Among other inputs, POMC neurons respond to leptin, a hormone synthesized in adipose and related cells in proportion to fat mass in the small intestine and then transmitted in blood to the hypothalamus.[14] Accordingly, POMC neurons signal satiety. A second population, consisting of AgRP neurons, responds to ghrelin synthesized in the stomach and duodenum, especially when no food is being digested (transmission from the stomach to the hypothalamus is likely via the vagus nerve, which has ghrelin receptors, and processed in the brainstem, with new ghrelin being synthesized in the arcuate nucleus). AgRP neurons also respond to other inputs indicating lack of food and so signal hunger.

Both POMC and AgRP neurons send outputs widely to other nuclei in the hypothalamus and locations elsewhere in the brain. One target is the lateral hypothalamic area (LHA). Neurons in the LHA promote feeding behavior and in 1998 two groups of researchers identified a neuropeptide synthesized in the LHA that specifically promotes feeding behavior. One group named it *orexin*,[15] the other *hypocretin*.[16] The name *orexin* is derived from the Greek word for appetite, signaling that it was assumed to be principally involved in initiating feeding behavior. Shortly after, however, other researchers revealed that these neurons also fire maximally before sleep-to-wake transitions and demonstrated that they promote these transitions. *Figure 1* indicates some of the known inputs and outputs of hypocretin neurons.

Hypocretin neurons represent the norm, not an exception, in the hypothalamus. They can be distinguished from one another in terms of their inputs, the peptides they synthesize, and patterns of connections, but in general hypothalamic neurons are not single purpose processors. Rather, each nucleus acts as a hub, integrating different information about the state of the organism and disseminating it to many other regions of the hypothalamus and elsewhere in the brain. As Saper and Lowell discuss,[17] there are hundreds, perhaps thousands of such cell populations. Such an in formation processing system is challenging to understand but plays a central role in coordinating vertebrate behavior both through interaction with

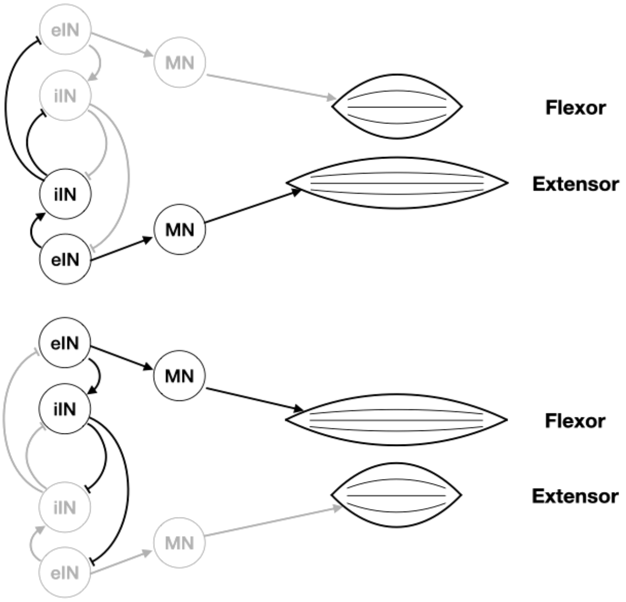

Figure 2. Local pattern generator controlling first contraction of the flexor muscle followed by contraction of the extensor muscle. In the top frame, the neurons in red are active, and the flexor inhibitory interneuron (iIN) inhibits both the extensor iIL and the excitatory inter neuron (eIN) as well as driving the flexor motor neuron (MN) which initiates contraction of the flexor muscle. When the activity of the flexor iIN neuron eventually wanes, the extensor iIN, eIN, and MN become active, and cause the extensor muscle to contract.

other brain regions and by directing the synthesis of hormones that directly regulate biochemical processes and behavioral activities. Among these activities are those involved in eating.

Before leaving the hypothalamus, I briefly note one nucleus that serves an important function in regulating nearly all activities of the organism. The suprachiasmatic nucleus (SCN, so named because of its location above the optic chiasm where neurons from the two eyes come together before distributing information to other brain regions) maintains an endogenous circadian (approximately 24 hour) rhythm. Although the rhythm is generated endogenously in individual SCN neurons, since the rhythm is only approximately 24-hours, their activity need to be regularly updated. Accordingly, they receive inputs both from the retina and neuropeptides released in other hypothalamic areas. SCN neurons then distribute this signal broadly, relying sometimes of electrical transmission along neurons and sometimes on neuropeptide dissemination, to tissues throughout the body. The peripheral cells use their circadian oscillation to regulate gene expression, expressing genes appropriate for the activities the cells need to perform at specific times of day. Among the areas regulated by circadian rhythms is the neocortex. As a result, performance of high-level cognitive activities varies over the course of a day.

The nuclei of the hypothalamus act as hubs that extend the information processing capacities of the endocrine system, integrating information from multiple sources and disseminating the resulting activity widely. In many cases the outputs consist of peptides that disseminate back into the bloodstream and function in the same manner as endocrines. In other cases, outputs are directed to other brain regions, including regions that can elicit motoric responses. Together, these nuclei provide an effective means of informing the various response capacities of the organism with information about when the conditions of the organism necessitate a response.

3 Pattern generators and locomotor regions: Controlling skeletal muscle

Many physiological activities (e.g., blood circulation, digestion) and all motor activities of animals require muscles. Individual muscle fibers can exert force by contracting, but a single muscle fiber acting on its own exerts insufficient force to perform the needed activity. Rather, many muscles must contract in a coordinated fashion. In recognition of this, Keijzer, van Duijn, and Lyon [18] argue that muscle coordination, not processing sensory inputs, was the activity for which neurons first evolved. Keijzer and colleagues appeal to the jellyfish as a model. In the jellyfish, locomotion results from rhythmic contractions of the bell made possible by two layers of contractile epithelial tissues (proto muscles). For the bell to contract and exert force, which allows the jellyfish to swim upwards, the proto muscles in these sheets must contract and then relax in unison. This is achieved by a network of neurons located between two layers of epithelial cells and pattern generating neurons organized in a ring that surrounds the bell.

The neurons surrounding the bell generate a

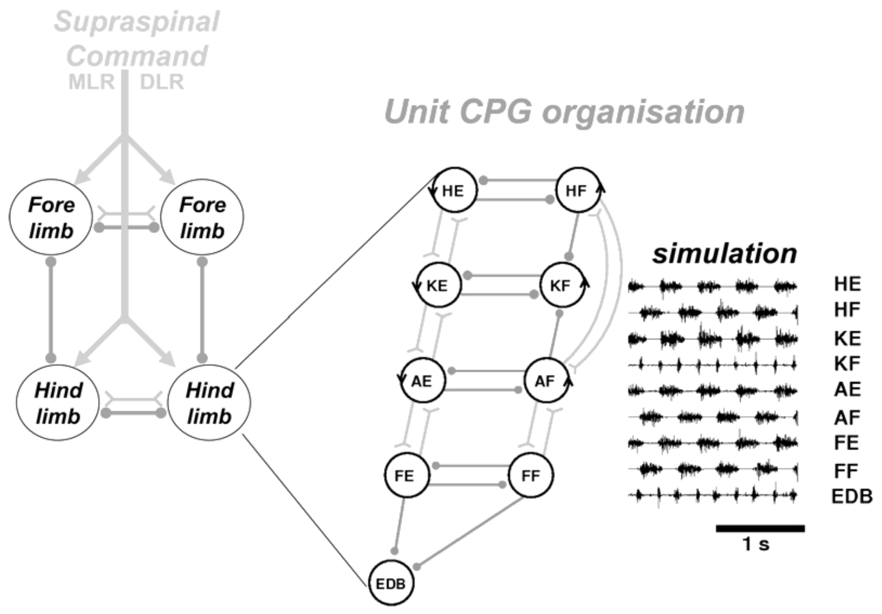

Figure 3. Interconnection of CPGs in a hindlimb of a vertebrate: hip (H), knee (K), ankle (A), and foot (F) extensors (E) or flexors (F). Extensor digitorum brevis (EDB) has a distinctive arrangement. Circles indicate inhibition, and forks/triangles excitation. Reprinted from S. Grillner, *Biological pattern generation: The cellular and computational logic of networks in motion*, p. 758. With permission from Elsevier.

rhythmic signal that is passed through the network, eliciting responses in all the proto-muscles at once. A similar arrangement of a nerve net controlling muscles is found in many vertebrate internal organs such as the lungs, heart, and those of the digestive tract.[19] In these networks, like that in the jellyfish, the oscillation is endogenously generated in the local circuits. It can be, and is, modulated by other neural signals, but the neural system regulating these muscles is not dependent on sensory input to initiate activity. In the case of vertebrate internal organs such as the lungs, heart, and those of the digestive tract, modulatory signals are transmitted from relevant nuclei in the hypothalamus through the autonomic nervous system, enabling, for example, increased breathing, circulation of blood, or eating when conditions in the organism require it.

The skeletal muscles that make motor activity possible in limbed vertebrates require more fine-grained regulation than just coordinated contraction: individual skeletal muscles must contract in a specific sequence to generate the needed limb movement. Nonetheless, similar organizing processes are employed, beginning with highly local control mechanisms. Skeletal muscles typically occur in pairs: flexor muscles contract the limb while extensor muscles restore the limb. These pairs are

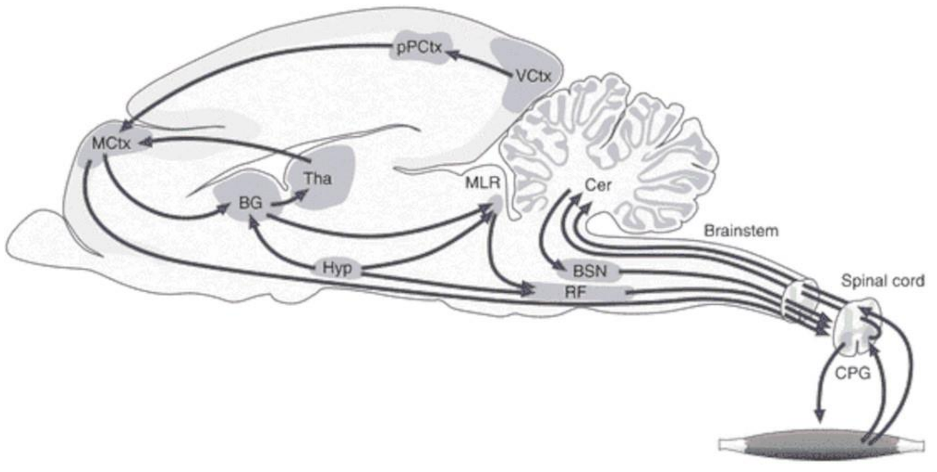

Figure 4. Major rain regions involved in controlling skeletal muscles in rodents. The most immediate control is exercised by central pattern generators (CPG) in the spinal cord, which are in turn integrated by a network in the reticular formation (RF). The mesencephalic local motor region (MLR) sends projections via the RF that direct specific actions. The MLR in turn receives inputs from both the hypothalamus (Hyp) and the basal ganglia (BG). Reprinted from O. Kiehn, K. Dougherty, *Locomotion: Circuits and physiology*, p. 1212. With permission from Springer Nature.

controlled locally to produce successive contractions and relaxations by central pattern generators (CPGs). These act on motor neurons that directly elicit contraction of a specific muscle fibers. In some cases, CPGs rely on intrinsically rhythmic neurons, but in many cases the rhythmic behavior results from the interaction between pairs of mutually inhibitory neurons, as in Figure 2. When one of the excitatory interneurons (eIN) is active, it activates both its motor neuron (MN) and an inhibitory interneuron (iIN) that suppresses both the excitatory and inhibitory interneurons controlling the other muscle. As its activity wanes, the other interneuron is released from inhibition, allowing it to activate its muscle and inhibit the first excitatory neuron.[20]

CPGs not only create rhythmic muscle contraction but serve as hubs for coordinating other inputs that affect muscle response. Locally, they receive somatosensory feedback from the muscles being controlled. This enables a CPG to, for example, register whatever resistance the muscle confronts and adjust muscle contraction in response.[21] In limbed organisms it is necessary to coordinate the movement of each limb in the pair. Accordingly, neuronal projections between CPGs on opposite sides of the body enable such coordination. Movement of whole limbs requires precise coordination between different muscle groups, which is typically achieved via interactions between multiple CPGs (*Figure 3*). These individual CPGs are not as rigidly connected as this suggests; different patterns of activity in the higher-level CPG can initiate different patterns in subordinate CPGs, and their activity can be further modified by neuromodulators (see section 5).

For control of skeletal muscles, peptidergic transmission is too slow. Transmitters such a glutamate and acetylcholine that elicit fast, ionotropic, responses are employed instead. Moreover, specific connectivity patterns are required to insure muscles contract in the right sequence. Networks within the spinal cord achieve these ends.[22] These networks are capable of coordinating muscle activity without any higher-level input. When Shik and Orlovsky[23] sectioned the spinal cord from the brain stem in kittens and placed them on a moving treadmill, they generated coordinated limb movements that adjusted appropriately as the speed of the treadmill was changed (e.g., transitioning between walking and running). This coordinated movement presumably reflected the coupling of individual CPGs. This is typically achieved through networks of neurons in the reticular formation that project down the reticulospinal tract. The name “reticular” means network and true to its name, the nuclei within the reticular formation form an extremely complex web. These networks are not well understood, but researchers have established that stimulating neurons in the lateral anterior reticular formation elicits coordinated movements, with different neurons eliciting different behaviors.[24]

As shown in *Figure 4*, the mesencephalic locomotor region (MLR) is a major source of input to the reticular formation.[25] When lesions are made above the MLR, stimulating neurons in it elicits coordinated walking or running behavior.[26] Roseberry and colleagues[27] determined that the MLR consists of multiple groups of neurons differentiated by reliance on different neurotransmitters. Serotonergic and glutamatergic neurons act to initiate muscle activity whereas GABAergic neurons slow muscle responses. Finally, stimulating cholinergic neurons modulates motor responses but does not initiate or inhibit them. The MLR thus appears as an integrating hub whose outputs result in specific motor activity and whose inputs serve to initiate, terminate, or modulate those activities.

In this section I have identified components of the architecture that regulates muscles. Critical to muscle action are the pattern generators responsible for each muscle and the network in which these are interconnected. Neurons at higher levels in the reticular formation and the MLR neurons are connected to specific CPGs and are able to elicit specific coordinated muscle contractions.

4 The basal ganglia: Selecting motor behaviors

In experimental protocols, nuclei in the MLR must be stimulated to produce motor responses. This is in significant part due to the activity of the output nuclei of the basal ganglia, the substantia nigra pars reticularis (SNr) and the globus pallidus interior (GPi). Neurons in these regions are tonically active and send inhibitory outputs not just to the MLR but to many brain regions, including those of the neocortex (*Figure 5*). Only when these inhibitory outputs are inhibited by processing in the basal ganglia, are neurons in the MLR (and other brain regions) released from inhibition and able to process information. The basal ganglia are thus an important control center that regulates information processing throughout the brain.

The basal ganglia are a set of interconnected nuclei located in the midbrain and base of the forebrain. They form a feedforward network from input nuclei to output nuclei. At a larger scale, the basal ganglia complete processing loops with other brain regions by sending outputs back to the same regions from which they receive inputs, either maintaining inhibition or releasing these areas from inhibition. (These loops also involve regions in the thalamus, which I will not discuss here.)

I focus on two pathways through which activity is directed through the different nuclei of the basal ganglia, one of which, the direct pathway, inhibits selected inhibitory neurons in the SNr and

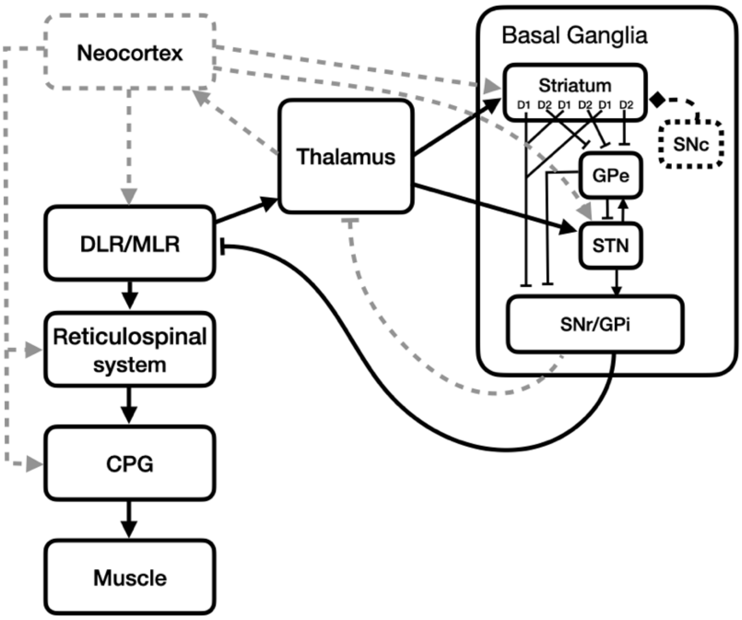

Figure 5. Organization of the Basal Ganglia and their role in control of processing in other brain areas. Components in black are active even without the neocortex, which, together with its connections to other regions, is shown in grey.

the GPi, while the other, the indirect pathway, further enhances their inhibitory outputs. The input neurons to both pathways reside in the striatum and are laid out topographically so that individual neurons receive inputs from specific regions in the brain. These input neurons also have one of two types of dopamine receptors, D1 or D2. I will return to the role of dopamine in the next section. For now, what is important is that D1 striatal neurons send their inhibitory output directly to specific SNr or GPi neurons (hence, this is known as the *direct pathway*); the result of inhibiting these neurons is to relax the inhibition of target areas. Thus, when a D1 neuron that receives input from a specific population in the MLR is activated, the inhibition of the MLR neurons is blocked and they become active and initiate muscle contraction. When D2 neurons in the striatum are activated, they send an inhibitory signal to neurons in the globus pallidus external (GPe), which in turn sends inhibitions to SNr or GPi output neurons (this is known as the *indirect pathway*). Processing in this pathway serves to reinforce the default inhibitory action of these output neurons. In the case of outputs that project to the MLR, activity in the indirect pathway serves to keep the muscles inactive.[28]

The two pathways in the basal ganglia provide a vehicle for selecting which other brain areas are allowed to function and which are inhibited. Which output neurons are active is in part determined by the relative strength of inputs to the D1 and D2 neurons. The competition is carried out through inhibitory neurons projecting between D1 and D2 neurons. The inputs to the striatum have limited bandwidth. Accordingly, the basal ganglia do not receive the information processed in these other areas; rather, the inputs it receives reflect the strength of the activity in the source/target regions. The basal ganglia constitute the site at which the competition between alternative neural processing is carried out. They enable the MLR neurons with the greatest activation to initiate muscle movement while those that would initiate competing muscle movements are suppressed.

The brain regions discussed so far provide an evaluation of needs of the organism and a means to select and control muscle activity. I have not considered how these regions are connected. The mediation is often accomplished through neuromodulators, to which I turn in the next section.

5 Neuromodulation: Setting agendas

The striatal neurons that are the inputs to the two pathways in the basal ganglia are differentiated by the type of dopamine receptor each possesses. Dopamine and other monoamines such as serotonin, are referred to as *neuromodulators* due to the roles they play in modulating neural circuits. Theorists sometimes assume that, as a result of a particular pattern of connections, neural circuits always process inputs in the same way. However, research on neural circuits in invertebrates challenged this view. Marder and her collaborators demonstrated that, depending on what neuromodulators are present, neurons in the lobster stomatogastric ganglion, responsible for the rhythmic contraction required for digestion of food, are organized into different coalitions realizing different behaviors.[29] In performing their roles as modulators, these molecules function differently than ionotropic neurotransmitters such as glutamate. In many respects these neuromodulators are similar to the neuropeptides described in section 2, which are sometimes also described as neuromodulators. They are released not just at synapses but from many regions in a neuron, including dendrites, and disseminate through the extracellular matrix to any neuron with an appropriate receptor. For a given neuromodulator there are multiple different receptor types that result in different responses by these target neurons to the same transmitter release. Katz offered a broad characterization of neuromodulation: «any communication between neurons, caused by release of a chemical, that is either not fast, or not point-to-point, or not simply excitation or inhibition».[30]

Before considering the role of neuromodulators more generally, I examine first how dopamine functions in the striatum of the basal ganglia. Dopamine is released into the dorsal striatum by neurons with cell bodies in the substantia nigra pars compactus (SNc). The D1 and D2 neurons are not only connected differently to neurons in other regions of the basal ganglia, but they respond to dopamine in opposite ways – D1 receptors respond to dopamine by bringing their resting potential closer to threshold, thereby making them more likely to generate action potentials and release their target from inhibition. D2 receptors respond in the opposite manner; in response to dopamine, they drive the resting potential further from threshold, making them less likely to respond. Dopamine thus biases the competition towards D1 neurons, making activity more likely.[31] In addition to regulating the likelihood of response, dopamine in the striatum is thought to play at least two other roles. Phasic dopamine release is hypothesized to constitute a reward signal that alters connectivity so that D1 neurons are more likely to respond to the same input in the future. When dopamine is increased tonically, on the other hand, it is hypothesized to enable activity in the circuit that is currently dominant, curtailing exploration of alternatives.[32]

Dopamine clearly modulates the activity of striatal neurons. Although the term *neuromodulator* captures this, it understates the systemic importance of neuromodulators. By determining how target circuits process information, neuromodulators configure the information-processing capacities of organisms. Accordingly, they might better be understood as setting the information-processing agenda. This role has been most clearly demonstrated in invertebrates. In the medicinal leach, serotonin increases activity in circuits leading to swimming behavior, whereas dopamine enhances activity in circuits supporting crawling.[33] There are receptors for dopamine, serotonin, and other neuromodulators, throughout vertebrate brains, including in the neocortex; they thus are situated in locations in which they are able to set the agenda for neural processing. Adopting such a broad perspective on the roles of dopamine on behavior, and tracing its role across phylogeny, Hills and his collaborators[34] have interpreted dopamine as functioning, across phylogeny, to promote search activities (search in new physical as well as in conceptual spaces).

While having widespread effects, neurotransmitters such as dopamine and serotonin are synthesized by neurons in only a few nuclei in the brain. In addition to the SNc, dopaminergic neurons are found in the ventral tegmental area (VTA) and several regions of the hypothalamus, including the arcuate nucleus discussed above. In the brain, serotonin is synthesized primarily in the nine raphe nuclei (it is also synthesized within the digestive tract). These various centers receive inputs from many other brain regions, including areas of the hypothalamus. Their axons then extend widely through the brain, from which the neuromodulator diffuses even more broadly. For example, dopaminergic neurons in the VTA project to the ventral striatum, nucleus accumbens, the amygdala, the hippocampus, the olfactory bulb, as well as the prefrontal cortex.[35] Neurons in the more rostral raphe nuclei project to areas in the midbrain and forebrain, while those in the more causal raphe nuclei project towards the brain stem and spinal cord (areas directly involved in initiating motor movements). The ways in which neuromodulators are synthesized and distributed, and their affects in determining processing in targeted neural circuits, enables them to set the information-processing agenda for much of the brain.

6 From the tectum to the neocortex: Coordinating sensory information

So far I have characterized how subcortical areas support assessing the condition of the organism, provide for and select between a range of motoric responses, and set the agenda for both neural activity and behavior through neuromodulators. With these resources, organisms are equipped to perform actions in the world in response to their current state. But for many actions to be successful the organism needs information about the layout of the world around it. Except for feedback to CPGs, I have ignored the neural processes that acquire this information. That is purposeful – when sensory processing is viewed as the starting point for cognitive processing that leads to action, it leaves fundamental questions unanswered: what moves organisms to act? and to act in one way rather than another? On the account I have advanced, processing components such as the hypothalamus and nuclei that synthesize neuromodulators motivate action. Sensory information is needed not to initiate action. Often its role is to refine already initiated subcortical processing directed at action as needed given what is available in the environment and how the organism is situated in its environment.[36] Identifying objects in the environment, their location, and the activities they afford are major functions of the neocortex. As I noted earlier, however, mammals like cats can live autonomously without a neocortex. They must still acquire and process sensory information and identify affordances. They do so using the optic tectum (commonly referred to as the superior colliculus in mammals).

The primary inputs to the optic tectum are from the retina. The tectum is organized in anatomical layers, each of which represents features of the environment in a topographic map constituting the animal's subjective perspective of the space in which it resides. These maps are aligned, but neurons in more superficial layers of the tectum have smaller receptive fields and respond solely to visual inputs, while those in deeper layers have larger receptive fields and integrate that information with other sensory information (auditory, somatosensory) and inputs from motor systems representing impending movements. Neurons in the tectum also receive inputs about the current needs of the organism, from which they can generate an assessment of the importance of different stimuli. The optic tectum is the hub of the midbrain stimulus selection network. Through its connections with other components of the network, it selects the identity and location of the stimulus of the greatest momentary importance.

The optic tectum sends outputs both to motor areas and to the thalamus and indirectly to the neocortex. The motor outputs suffice both to orient the organism with respect to selected stimuli and to engage in feeding or defensive activities, including fleeing.[37] These are presumably what enable decorticated mammals to respond to visual and other sensory input.[38] The pathways from the tectum to the neocortex suggests that once the neocortex evolved, the tectum and neocortex could operate together. The neocortex is in an important respect organized in the same manner as the optic tectum with successive maps of stimulus space, each with larger receptive fields, aligned with each other. Instead of being stacked on top of each other, they are laid out as different cortical areas. The maps in the neocortex are more expansive than those in the tectum, allowing for greater processing capacity. In addition, through interactions between the thalamus and regions of neocortex, different areas can be invoked when their information-processing capacities are relevant.

In neural network modeling, the neocortex is treated as a single, comprehensive processing system that processes sensory inputs to arrive at outputs that categorize information or, if models include frontal areas of the brain, direct motor activity. This corresponds to how, in the actual neocortex, visual stimuli are first processed in V1, then in two different streams, one emphasizing identification of objects, the other location in space and potential for action.[39] As insightful as this approach is to understanding processing of visual stimuli, it fails to take into account how each of the regions of the neocortex is integrated with other brain regions. This interconnection is seen in the loops through which areas of the neocortex are connected to the basal ganglia and thalamus as well as by the projection of neuromodulators to various areas in the neocortex. This suggests that, in addition to the forward and recurrent projections between cortical areas, each area is coordinated in its own way with subcortical areas. Like the tectum, it carries out this processing through interconnections with subcortical regions, including those discussed in earlier sections. These processes can only be understood by addressing the interconnection of cortical areas with subcortical ones. From such a perspective, one can appreciate both how specialized processing in neocortical areas contributes to processing elsewhere in the brain and how processing in those areas affects processing in the neocortex.

While I am emphasizing subcortical information processing and its integration with cortical processing, it is important to note that the architecture of the neocortex allows for distinctive information processing capacities. The ability to categorize objects and apply knowledge acquired about categories to individual instances is extremely important in human life and appears to be a distinctive capacity of the neocortex. A further distinctive ability is to learn natural languages and deploy them in reasoning. This enables coordinated cognitive investigations between humans, such as scientific inquiries that exceed what members of other species can accomplish. It also enables humans to think about their own thinking, engaging in what Karmiloff-Smith[40] describes as *representational redescription* and is more generally characterized as *metacognition*. One capacity this makes possible is for humans to construct narratives about themselves and invoke such narratives in regulating their lives.[41] Recognizing and investigating the types of cognition the neocortex makes possible, however, does not require viewing it as operating autonomously from the rest of the brain. Rather, once one recognizes the role processing in other brain areas figures in identifying states of the organism (e.g., hunger, thirst, fear, etc.) and coordinating behavioral activities, one can explore how higher-level cognitive activities coordinate with these. Moreover, insofar as a great deal of relevant information processing is carried out by other brain structures, one can look for and localize in the neocortex the specialized information processing it performs while localizing other information processing that contributes to overall cognitive activities elsewhere in the brain.

7 Conclusion: Vertebrate cognition employs a heterarchy of different cognitive architectures

Once we recognize that there are many different information processing systems in the vertebrate brain and that their different activities are integrated in regulating behavior, we should rethink the types of cognitive architectures invoked in cognitive science. Instead of identifying a single architecture, modeled on the neocortex, we should seek to understand the different architectures that process information in the vertebrate brain and how they are coupled together.

I started with the subcortical processes that evaluate an organism's state and that direct muscle action. These employ different architectures for information processing. The hypothalamus extends the chemical processing architecture of the endocrine system and brainstem areas such as the nucleus of the solitary tract, providing a network of hubs that integrate signals specifying different conditions of the organism that may require responses. CPGs and the MLR are configured in a different manner, one suited to generate a temporal ordering of processing both in individual muscles and between muscles. The basal ganglia provide yet another architecture, one suited to carrying out a competition in which circuits with the strongest activation are released from inhibition and allowed to proceed with processing information. Attending to the role of dopamine receptors in the striatum of the basal ganglia reveals the more general role neuromodulators play in determining how different brain areas work on different occasions.

Only after introducing these regions, I turned to the information processing of sensory stimuli. In early vertebrates, this involved the optic tectum/superior colliculus mapping stimulation from the environment onto motor responses. In doing this, the tectum both receives inputs and sends outputs to these other subcortical areas. In higher mammals the neocortex takes on much of analysis of sensory inputs, but it contributes in much the same manner as the optic tectum, supplying information about the layout of the environment and objects in it that can support activity often initiated by subcortical components.

Accounts of cognitive architectures, whether symbolic or neural network, have generally focused on the resources thought to be needed to perform high-level information processing such as abstract reasoning and problem solving. These accounts support the view that cognition is simply engaged in these high-level, abstractly specified tasks. The subcortical components on which I have focused support a different perspective – the main task for which information processing is required is the maintenance of the organism. This requires assessing the state of the organism, selecting between possible actions, and coordinating muscles so as to carry out selected actions. The processing of sensory information in the neocortex allows for abstract reasoning that exceeds the immediate needs of the organism. Even that activity, however, is carried out in an integrated system in which, for example, decisions as to what information to consider are made using the basal ganglia, and the neural processes are themselves subject to agendas set by neuromodulators.

Having identified multiple information-processing architectures in the brain, a major question emerges: how are these different systems organized so as to work together? In designing systems in which multiple components need to work together effectively, theorists often turn to hierarchical designs in which multiple lower-level units report to a single higher-level unit, and ultimately one top-level unit oversees the whole system. The different units are organized into a pyramid. Hierarchical organization is often implemented in social systems and in human-made artifacts. It is common to characterize the brain as similarly hierarchically organized, with sensory areas processing input information, passing it to higher processing centers, ultimately reaching a central executive thought to be located in the prefrontal cortex. Once the prefrontal cortex arrives at a plan of action, commands are directed down the hierarchy until they are implemented by muscles. On this scheme, the information processing architectures I have identified are ultimately subordinate to and controlled by the neocortex, and ultimately by the prefrontal cortex.

Hierarchy is not the only possible way of organizing component systems. I use the term *heterarchy* to describe organization that violates one or more features of hierarchical organization.[42] For purposes here, the crucial departure from hierarchy is that different units are not subordinate to a common higher-level unit. Rather than forming a hierarchical pyramid, the components constitute a network in which different components, operating by their own principles, carry out their activity while also influencing each other.[43] Coherent behavior of the whole organism results not from a central executive making all the decisions, but from coordination between the components. The hypothalamus, among other areas, registers needs of the organism, regions releasing neuromodulators such as serotonin and dopamine set the agendas for other areas, the basal ganglia allow for decisions between alternatives, and motor areas determine how actions are carried out. The neocortex carries out specific processing, especially of stimuli, and constructs memories and accesses stored information, but these processes are not in charge of other processing. Rather, they participate in the network in which behavioral is ultimately generated.

One reason that theorists often default to assuming hierarchical organization is that they assume that allowing components each to operate according to its own procedures will lead to conflict and overall dysfunction. It is certainly the case that non-hierarchical systems can engage in conflict and even be dysfunctional, although hierarchical systems can also be dysfunctional. One factor that can mitigate concerns about dysfunctionality is that the organization of brain networks is a product of evolution. Only those organisms in which brain networks enabled the organisms to maintain themselves in their environments long enough to reproduce were inherited. Considering evolution provides a further reason to expect heterarchical organization. The basic organization of the vertebrate brain was in place in the last common ancestor of all of today's vertebrates. What has evolved since then are a large number of variants on this architecture, each deriving from another by "tinkering" with earlier designs.[44] A process of tinkering with extant designs is not likely to generate hierarchy and may undercut existing hierarchical design. If developed gradually over a prolonged period of evolution, however, it may produce a highly robust information-processing system.[45]

The structure that has undergone the most change in the vertebrate lineage is the pallium, a three-layer structure that expanded into the six-layer neocortex, which has in turn diversified into a host of different regions. As I have emphasized throughout, each of these has maintained interactions with the thalamus, basal ganglia, and other subcortical structures. It is common to construe neocortical areas as processing informationally sequentially (e.g., from primary visual cortex along streams in the inferotemporal cortex and the parietal cortex). These streams continue into the prefrontal cortex, with inferotemporal areas supplying inputs to areas involved in evaluation and parietal areas supplying inputs to areas engaged in associations between stimuli and actions and pragmatic, social, and moral norms affecting action.[46] But, as Felleman and van Essen showed,[47] there are also many interconnections between the streams and there are typically more recurrent than forward projections. Recent research has revealed complex dynamical behavior within the cortex such as traveling waves that affect how information is processed in specific brain regions.[48] These and other cortical oscillations are partly driven by interactions between cortical regions and regions of the thalamus. These findings all point to a heterarchical organization involving multiple interacting components arrived at via tinkering with earlier designs.

Approaching information processing in the brain in the way I have builds on the view that cognition is in the service of the organism, regulating activities it needs to perform to maintain itself. From this perspective, the forms of information processing that have been the focus of cognitive science – categorization, language production and comprehension, memory encoding and retrieval, problem solving, metacognitive processing, etc. – remain important. The neocortex plays a critical role in these processes. But these processes are integrated into a larger system, one that is more directly tied to the maintenance of the organism. Higher cognitive processes do not exhaust the information processing vertebrates employ to control their behavior. And they are not carried out independently of these other information processing activities that employ brain structures exhibiting different architectures. To understand the different types of information processing that vertebrates perform, cognitive science needs to characterize the diverse information-processing architectures found in the brain and investigate how they coordinate with each other in generating behavior.

Notes

[1] Cf. A. Newell, *Physical symbol systems*. In: «Cognitive Science», vol. IV, n. 2, 1980, pp. 135-183; A. Newell, *Unified theories of cognition*, Harvard University Press, Cambridge (MA) 1990.

[2] Cf. D.E. Rumelhart, J.L. McClelland (eds.), *Parallel distributed processing: Explorations in the microstructure of cognition. Vol. I, Foundations*.

[3] Cf. D.L.K. Yamins, J.J. Di Carlo, *Using goal-driven deep learning models to understand sensory cortex*; C. Zhuang, S. Yan, A. Nayebi, M. Schrimpf, M.C. Frank, J.J. Di Carlo, D.L.K. Yamins, *Unsupervised neural network models of the ventral visual stream*.

[4] Cf. H.R. Maturana, F.J. Varela, *Autopoiesis and cognition: The realization of the living*.

[5] Cf. W. Bechtel, L. Bich, *Grounding cognition: Heterarchical control mechanisms in biology*.

[6] Cf. P. Lyon, F. Keijzer, D. Arendt, M. Levin, *Reframing cognition: Getting down to biological basics*.

[7] Cf. S. Grillner, *Evolution of the vertebrate motor system - from forebrain to spinal cord*.

[8] Cf. L.M. Bjursten, K. Norrsell, U. Norrsell, *Behavioural repertory of cats without cerebral cortex from infancy*.

[9] Cf. L.T.-L. Huang, L. Bich, W. Bechtel, *Model organisms for studying decision-making: A phylogenetically expanded perspective*.

[10] Cf. J.A. Fodor, *The language of thought*.

[11] Cf. A. Newell, H.A. Simon, *Human problem solving*.

[12] Cf. D.C. Dennett, *Real patterns*.

[13] Cf. B. Kleine, W.G. Rossmanith, *Hormones and the endocrine system: Textbook of endocrinology*.

[14] For a historical review of the discovery and research on leptin, cf. D.L. Coleman, *A historical perspective on leptin*. Leptin also acts as an endocrine, producing effects on blood glucose levels similar to those of insulin (cf. A.A. da Silva, J.M. do Carmo, J.E. Hall, *CNS regulation of glucose homeostasis: Role of the leptin-melanocortin system*).

[15] Cf. T. Sakurai, A. Amemiya, M. Ishii, I. Matsuzaki, R.M. Chemelli, H. Tanaka, S.C. Williams, J.A. Rich-

ardson, G.P. Kozlowski, S. Wilson, J.R. Arch, R.E. Buckingham, A.C. Haynes, S.A. Carr, R.S. Annan, D.E. McNulty, W.S. liu, J.A. Terrett, N.A. Hlshourbagy, D.J. Bergsma, M. Yanagisawa, *Orexins and orexin receptors: A mamily of hypothalamic neuropeptides and G protein-coupled receptors that regulate feeding behavior*.

[16] Cf. L. de Lecea, T.S. Kilduff, C. Peyron, X.B. Gao, P.E. Foye, P.E. Danielson, C. Fukuhara, E.L.F. Battenberg, V.T. Gautvik, F.S. Bartlett II, W.N. Frankel, A.N. van den Pol, F.E. Bloom, K.M. Gautvik, J.G. Sutcliffe, *The hypocretins: Hypothalamus-specific peptides with neuroexcitatory activity*.

[17] Cf. C.B. Saper, B.B. Lowell, *The hypothalamus*.

[18] Cf. F. Keijzer, M. van Duijn, P. Lyon, *What nervous systems do: Early evolution, input-output, and the skin brain thesis*.

[19] Keijzer and colleagues focus on the locomotive activities of jellyfish. But other theorists, focusing on Hydra, which belong to the same phylum as jellyfish, *Cnidaria*, emphasize digestive activities and interpret the primary function of the nerve net as directing nutrients through the digestive system of the hydra much as the enteric nervous system does in us. As a result, Furness and Stebbing argue that the enteric nervous system, often viewed as a second brain, is in fact the descendent of the first brain (cf. J.B. Furness, M.J. Stebbing, *The first brain: Species comparisons and evolutionary implications for the enteric and central nervous systems*).

[20] Cf. D. Bucher, G. Haspel, J. Golowasch, F. Nadim, *Central pattern generators*.

[21] Cf. I. Steuer, P.A. Guertin, *Central pattern generators in the brainstem and spinal cord: an overview of basic principles, similarities and differences*.

[22] Cf. O. Kiehn, *Decoding the organization of spinal circuits that control locomotion*.

[23] Cf. M.L. Shik, G.N. Orlovsky, *Neurophysiology of locomotor automatism*.

[24] Cf. R.M. Brownstone, J.W. Chopek, *Reticulospinal systems for tuning motor commands*.

[25] Cf. U. Sławińska, L.M. Jordan, *Serotonergic influences on locomotor circuits*.

[26] Cf. I. Steuer, P.A. Guertin, *Central pattern generators in the brainstem and spinal cord: An overview of basic principles, similarities and differences*.

[27] Cf. T.K. Roseberry, A.M. Lee, A.L. Lalive, L. Wilbrecht, A. Bonci, A.C. Kreitzer, *Cell-type-specific control of brainstem locomotor circuits by basal ganglia*.

[28] Cf. T.K. Roseberry, A.M. Lee, A.L. Lalive, L. Wilbrecht, A. Bonci, A.C. Kreitzer, *Cell-type-specific control of brainstem locomotor circuits by basal ganglia*.

[29] For a succint review, cf. E. Marder, *Neuromodulation of neuronal circuits: Back to the future*.

[30] P.S. Katz, *What are we talking about? Modes of neuronal communication*. In: P.S. Katz (ed.), *Beyond neurotransmission: Neuromodulation and its importance for information processing*, p. 3.

[31] Cf. T.K. Roseberry, A.M. Lee, A.L. Lalive, L. Wilbrecht, A. Bonci, A.C. Kreitzer, *Cell-type-specific control of brainstem locomotor circuits by basal ganglia*.

[32] Cf. T.T. Hills, P.M. Todd, D. Lazer, A.D. Redish, I.D. Couzin, the Cognitive Search Research Group, *Exploration versus exploitation in space, mind, and society*.

[33] Cf. J.G. Puhl, K.A. Mesce, *Dopamine activates the motor pattern for crawling in the medicinal leech*.

[34] Cf. T.T. Hills, P.M. Todd, R.L. Goldstone, *Search in external and internal spaces: Evidence for generalized cognitive search processes*; T.T. Hills, P.M. Todd, D. Lazer, A.D. Redish, I.D. Couzin, the Cognitive Search Research Group, *Exploration versus exploitation in space, mind, and society*.

[35] Dopaminergic neurons from the arcuate nucleus as well as the periventricular nucleus of the hypothalamus project to the pituitary and act to inhibit the secretion of prolactin, a protein that enables milk production.

[36] This is not to deny that sensory signals sometimes initiate action. An anonymous reviewer pointed to the role of sensory inputs generating aesthetic evaluation. So far most research on neural processing of aesthetic stimuli has focused on areas of the neocortex, although there has been some research addressing the role of dopamine processing in the striatum (cf. S. Lacey, H. Hagtvedt, V.M. Patrick, A. Anderson, R. Stilla, G. Deshpande, X. Hu, J.R. Sato, S. Reddy, K. Sathian, *Art for reward's sake: Visual art recruits the ventral striatum*).

[37] Cf. E. Comoli, P. Das Neves Favaro, N. Vautrelle, M. Leriche, P.G. Overton, P. Redgrave, *Segregated anatomical input to sub-regions of the rodent superior colliculus associated with approach and defense*.

[38] Cf. B.E. Stein, M.A. Meredith, *The merging of the senses*.

[39] Cf. D.C. van Essen, J.L. Gallant, *Neural mechanisms of form and motion processing in the primate visual system*.

[40] Cf. A. Karmiloff-Smith, *Beyond modularity*.

[41] Cf. W. Bechtel, *Mental mechanisms. Philosophical perspectives on cognitive neuroscience*, pp. 239-268.

[42] The term was introduced by McCulloch (cf. W.S. McCulloch, *A heterarchy of values determined by the topology of nervous nets*) for preferences that form circles (A is preferred to B, B to C, and C to A). Pattee extended the concept to control mechanisms when they deviate from a hierarchy (cf. H.H. Pattee, *Measurement-control heterarchical networks in living systems*). Heterarchical organization can differ from hierarchy in multiple ways – there can be more units at higher levels than at lower levels, inverting the pyramid, and when units exercise control over others, multiple ones may control the same component and controlled components can, in some respects, exercise control over those taken to be in control (cf. W. Bechtel, *Levels in biological organisms: Hierarchy of production mechanisms, heterarchy of control mechanisms*).

[43] Cf. W. Bechtel, *Levels in biological organisms: Hierarchy of production mechanisms, heterarchy of control mechanisms*.

[44] Cf. F. Jacob, *Evolution and tinkering*.

[45] Cf. L. Bich, W. Bechtel, *Control mechanisms: Explaining the integration and versatility of biological organisms*.

[46] Cf. R.W. Carlson, M.J. Crockett, *The lateral prefrontal cortex and moral goal pursuit*.

[47] Cf. D.J. Felleman, D.C. van Essen, *Distributed hierarchical processing in the primate cerebral cortex*.

[48] Cf. Z.W. Davis, L. Muller, J. Martinez-Trujillo, T. Sejnowski, J.H. Reynolds, *Spontaneous travelling cortical waves gate perception in behaving primates*.

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