

# Neural Population Computing: Parallel Distributed Processing, the Basal Ganglia, and Evolution

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## Abstract

Representations in the central nervous system are population encoded. Understanding the computational processes subserved by pools of cortical and connected subcortical neurons constitutes one of the major challenges facing systems neuroscience. The science of parallel distributed processing (PDP) combines neural plausibility, theoretical coherence, and a demonstrated ability to account for an enormous range of phenomena in normal and damaged human brains. PDP features have now been demonstrated in mice and *Hydra*. I here discuss a recently introduced granular PDP model of the basal ganglia (BG) that takes into account the fundamental anatomic and neurophysiologic features of the component structures and logically accounts for the effects of low dopamine levels as observed in Parkinson's disease (PD). Research on lamprey and *Drosophila* suggests that the essential computational function of the sensorimotor BG (smBG) is reduction of a high dimensionality input space (sensory, motor, and internal drives) to a low dimensionality output space comprised of a limited portfolio of mutually compatible behaviors. Optimization is achieved in the process of iterative settling into a constellation of attractor states. An evolutionary perspective suggests that, for much of the history of complex nervous systems, dating back to arthropod precursors, the smBG, in conjunction with PDP, has provided the basis for the most fundamental of computational functions, reactive intention: the automatic translation of available afferent information into an optimal behavioral response. Experience with pallidotomy for treatment of PD suggests that, in humans, the smBG has become largely anachronistic, its function superseded by cortical mechanisms.

**Keywords:** Parallel distributed processing, Population encoding, Attractor, Basal ganglia, Brain evolution, Lamprey, *Drosophila*

## Introduction

It has been known for some time that representations in the central nervous system (CNS) are population encoded, that is, encoded as patterns of activity involving very large numbers of highly interconnected neurons in one or more neural networks extending over large expanses of the brain [1-11]. Nonetheless, understanding the computational processes occurring in pools of cortical neurons and the subcortical nuclei with which they interact continues to be one of the major challenges facing systems neuroscience.

The science of parallel distributed processing (PDP) [12] provides a means for addressing this challenge. The underlying mathematics were developed by Hopfield and Tan [13]. PDP has theoretical coherence and neurological verisimilitude and it has been able to account for a large number of cognitive phenomena in

normal people, including reaction times (and reading latencies), stimulus recognition, the effect of stimulus salience on attention, perceptual invariance, simultaneous egocentric and allocentric visual processing, top-down/bottom up processing, language errors, the effect of statistical regularities of experience, frequency, and age of acquisition, instantiation of rules and symbols, content addressable memory and the capacity for pattern completion, preservation of function in the face of noisy or distorted input, inference, parallel constraint satisfaction, the binding problem and gamma coherence, principles of hippocampal function, the location of knowledge in the brain, limitations in the scope and depth of knowledge acquired through experience, and Piagetian stages of cognitive development [14]. PDP principles have been able to provide a coherent account for impairment in a variety of language functions resulting from stroke or dementia in a large number of languages and the phenomenon of graceful

degradation observed in such studies [15,16]. They have also made important contributions to our understanding of attention (including hemispatial neglect), emotional function, executive function, motor planning, visual processing, decision making, and neuroeconomics [14].

Until recently, PDP was a theoretical construct, validated almost exclusively in human studies. However, Yuste and his colleagues [17-19], using calcium imaging, have now demonstrated cardinal PDP principles in operation in the visual cortex of awake, behaving mice: acquisition of knowledge of statistical regularities of experience, population encoding, attractor states, and pattern completion (see also parallel work [20-23]).

While PDP has enormously advanced our understanding of cortical function [7], its single greatest accomplishment may be its contribution to our understanding of the computational processes subserved by the hippocampus and connected mesial temporal structures [7] (see brief review [14]). In a recent paper, I took a comparably granular approach to analyzing basal ganglia (BG) function [24]. This approach substantially illuminated the computational function of the BG but review of the pallidotomy literature also suggested that the sensorimotor BG (smBG) (dorsal head of caudate, body and tail of caudate, and putamen) have become an anachronism in humans, its computational function supplanted by cortical processes. Research on the lamprey, a jawless fish that departed from the mammalian line 560 million years ago, and pioneering work by Fiore and his colleagues [25], subsuming review of deep homologies between major components of the central complex of the lamprey, *Drosophila*, and primate brain, provided two fundamental insights: 1) the fundamental computational function of the BG is dimensionality reduction; and 2) PDP processes date back at least to arthropods and may constitute the computational principle shared by all creatures with complex nervous systems. In this paper, I briefly review a BG model and these insights garnered from studies of far more primitive creatures.

## The Sensorimotor Basal Ganglia

A somewhat simplistic model of the smBG is depicted in the figure [24]. The model incorporates several key assumptions: 1) recurrent collaterals in the cortex provide the basis for settling within attractor basins into attractor states; 2) recurrent collaterals in the striatum, globus pallidus externa (GPe), and globus pallidus interna (GPi), all of which are comprised predominantly of GABAergic neurons, provide the basis for competitive inhibition and winner-take-all computational dynamics; 3) whereas none of the subcortical structures has the extensive interconnectivity (i.e., dense coding) that is fundamental to cerebral cortical function, there is some dispersion of

input and/or output provided by dendritic and axonal arborizations (double lines in Figure); this is particularly true of the GPe and GPi, in which dendritic arborizations are enormous, spanning 1.5 mm [26]; and 4) central nervous system processing (CNS) consists of sequential settling into constellations of attractor states within attractor basins generated throughout the CNS; this settling process is achieved by innumerable back and forth volleys of neural transmission (transmission time from the frontal pole to the occipital pole of the human brain is likely on the order of 2 ms), governed in the cortex by processes involved in achieving gamma synchrony [27]; in the course of these back and forth volleys, the limited dispersion provided by dendritic and axonal arborizations is multiplied many-fold such that the entire smBG is recruited, settling occurs, and parallel constraint satisfaction is achieved.

The model also assumes two major populations of GABAergic neurons in the striatum, one giving rise to the “direct” pathway, the other to the “indirect pathway” [28]. Direct pathway striatal neurons project to GPe and GPi. Dopamine, acting at D1 receptors, renders them *more* excitable by cortical glutamatergic input. Indirect pathway striatal neurons project nearly exclusively to GPe, which in turn projects to STN, which projects to GPi. Dopamine, acting at D2 receptors, renders indirect pathway striatal neurons *less* excitable.

This simple model provides the basis for a settling process involving all of the structures in the model (an attractor “trench”) that eventuates, over perhaps a hundred volleys, in the achievement of one or more attractor states in the cortical targets of the thalamus. Dopamine, by virtue of its opposite actions on the two GABAergic populations in the striatum, regulates both the number of states and the depth of the cortical attractor basins. High dopamine levels in the striatum will promote the generation of multiple motorically compatible attractor basins and will maximize the depth of these basins. Low dopamine levels will minimize the number of attractor basins (the explanation for the impairment in simultaneous or temporally closely sequenced movements exhibited by patients with Parkinson’s disease (PD) [29,30]), and minimize their depth (hence the hypometria and bradykinesia of patients with PD). Increases in dopamine facilitate behavioral switches (by expanding the repertoire of attractor trenches) while decreases in dopamine retard switching (as shown [31]).

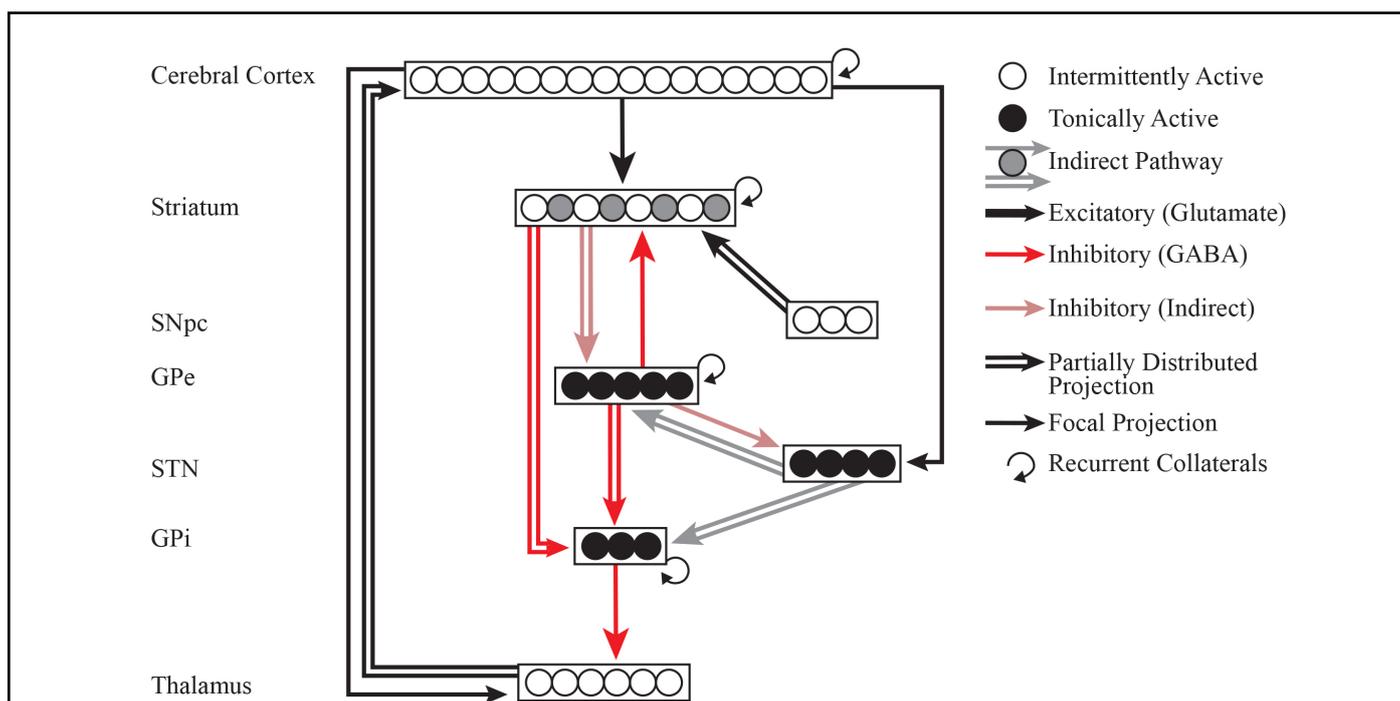
## The Evolutionary Perspective

An exact homology can be drawn between every aspect of BG structure, connectivity, neural organization, ion channels, and neurotransmitters in humans and the lamprey, the phylogenetically oldest group of living vertebrates to have diverged from the mammalian

evolutionary line [32-34]. Extensive homology can be drawn between the BG of humans and lampreys and the insect central complex (e.g., in *Drosophila*), including embryological derivation, orthologous genetic specification, neural architecture, neurochemical attributes (including the modulating influence of dopamine), physiological properties, and behavioral outcomes of neural activity [25,35]. The common thread linking structure and function in these disparate creatures is dimensionality reduction [25]: sensory inputs define a complex, high dimensionality space that must be optimally translated into a low dimensionality space corresponding to a limited repertoire of possible behavioral responses (see also [36]). For example, the lamprey receives rich visual, vestibular, auditory, somatosensory, olfactory, and lateral line organ input of different types from various regions in space (suggestion the adaptive value of rich multimodal sensory input), as well as neural input reflecting the current state of its motor system and internal drives (e.g., hunger, sexual urge), and it must translate this into swimming forward or backward, lateral and vertical bending movements, mouth movements (biting and sucking), and release of eggs or sperm [32]. In computational terms, sensory

input defines, through the BG/central complex, specific positions within an attractor trench landscape in which attractor state constellations and behaviors are achieved that constitute optimal responses to extremely complex, multimodal patterns of sensory input without incurring mutually incompatible behaviors [25].

The adaptive value of such a mechanism provides a robust explanation for its evolutionary conservation dating back at least to arthropods. Evidence of a neurological basis for attractor dynamics has recently been reported in *Drosophila* [37-40]. Dupre and Yuste [41] have provided evidence of population encoding (but not attractor neurodynamics) in *Hydra vulgaris*, a far more primitive invertebrate classed in the phylum Cnidaria, which includes jelly fish. These observations suggest that PDP may be the computational mechanism underlying neural function in all creatures with multicellular nervous systems, evolutionarily conserved through perhaps a billion years because of its adaptive value. They also illuminate the central role that the BG has played throughout much of the evolution of complex creatures: reactive intention — automatic responses to configurations of sensory input [24].



**Figure 1:** The model, a pattern associator network, attempts to capture the major features of connectivity and distribution of representations [24]. In any computer simulation of such a model, each structure would have a far larger number of units and the ratios of units in the various structures would be greater (e.g., the striatum has 12 times the volume of GPe and 20 times that of GPi [43] and the volume of the cortex projecting to the striatum is vastly greater than that of the striatum itself). The circles with arrows at the end of some domains (cerebral cortex, striatum, GPe, and GPi) indicate recurrent connections. In the cortex, these are excitatory and provide the basis for settling into attractor states. In the striatum and GP, they are inhibitory and provide the basis for competitive inhibition and its computational effects (see text). Distributed connections (represented as double lines), whether reflecting projection from multiple sites to a single target cell or region (e.g., the cerebral cortex), or projection to multiple target cells (e.g., the pallidum) confer the capacity for acquisition of knowledge of regularities in experience and are crucial to attractor basin/trench dynamics.

## Conclusion

This brief review has elucidated, using a simple PDP-inspired model, the essential computational function of the BG. Given the architectural similarities between the smBG and the rostroventral basal ganglia (rvBG) — the portion incorporating the ventral head of the caudate nucleus and nucleus accumbens, we can assume that the rvBG serves a similar purpose of dimensionality reduction. However, the dimensions being reduced — the province of dorsolateral and orbitofrontal cortex — are unclear. Furthermore, we have neither animal models nor human selective lesion models to guide us.

As I have detailed, data emerging from animal studies (mice, lamprey, *Drosophila*, *Hydra*) suggest that PDP may provide the fundamental basis for CNS computation in all creatures with multicellular nervous systems.

The evidence suggests that the smBG has been the lynchpin of CNS function for perhaps as much as a billion years. How is it possible, then, to say that the smBG has become an anachronism in humans — a structure that serves no useful purpose but can wreak havoc when its function is impaired? This conclusion was based upon four considerations: 1) well-placed lesions in the middle of the posteroventral aspect of the GPi are almost definitive in their relief of Parkinsonian symptoms and apparently at no clinical cost; 2) the cortex (vestigial in lamprey) has become so large and the behavioral repertoire so expansive in humans that the necessity for dimensionality reduction has been markedly reduced; 3) we have extensive evidence of cortical systems, well developed in higher animals, particularly primates, subserving dimensionality reduction: working memory and volitional and reactive attention; and 4) much of human behavior is volitional, not automatic, driven by the dorsolateral frontal cortex, which is informed of objective knowledge and perceptual input by postcentral cortices and of subjective knowledge and limbic input from orbitofrontal cortex [42]. These considerations compel us to view the nervous system of any creature in an entirely different way: to understand that any structure, pattern of connectivity, neuron type, or neurotransmitter receptor may still have adaptational value, or it may be an evolutionary relic.

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## Conflicts of interest

The author has no conflicts of interest bearing on this manuscript.

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