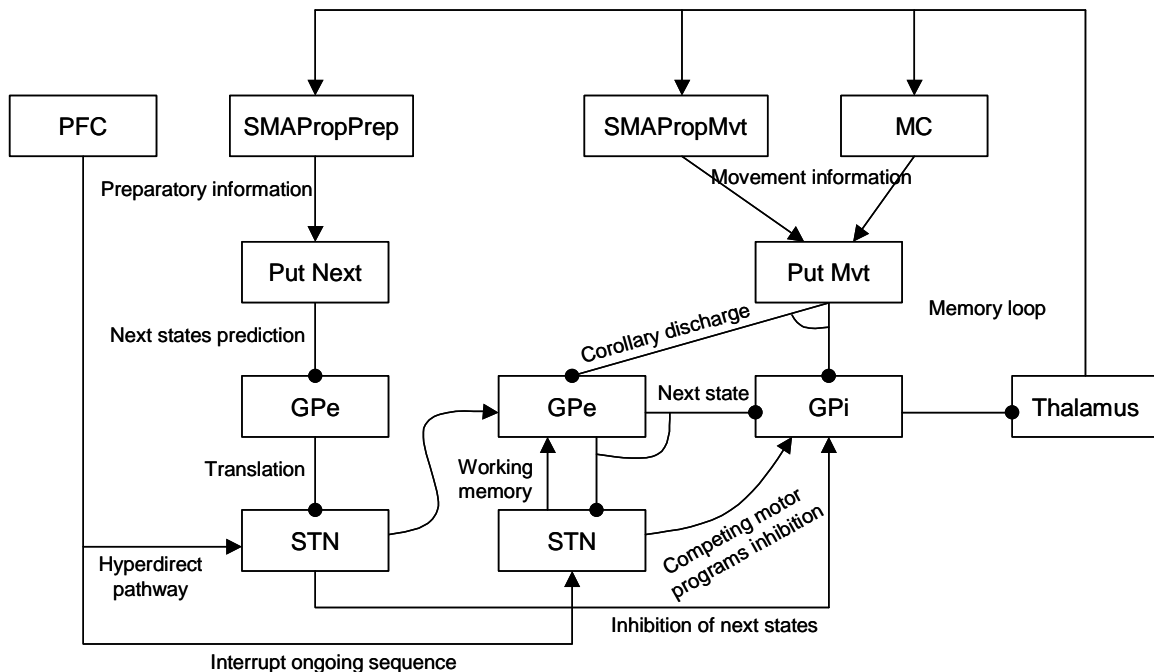


A Basal Ganglia Model for the Execution of Sequences of Motor Programs

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It has long been proposed that the basal ganglia (BG) play a role in sequential learning (Marsden and Obeso, 1994). Comparative studies show that the BG carry out at least 3 functions: learning patterns of motor activity that yield a reward; play a part in sequencing the individual elements that constitute a motor program; interrupt an ongoing sequence contingent on external events signaled by sensory inputs (Lieberman, 2000). One of the most popular models has been the proposed by Albin and DeLong (Albin et al., 1989; DeLong, 1990). On it, the BG process information through two segregated pathways, the ‘direct’ and ‘indirect’, having opposite effects on the BG output. The equilibrium between both paths would be modulated by dopamine influencing different receptors: D1 and D2. Recent neuroanatomical findings (Parent et al., 2000) have shown that this view is no longer valid. Extensive axonal collateralization in the striatofugal system is incongruent with the idea that there are separate and discrete direct and indirect systems; practically all striatal neurons send collaterals to the external segment of the globus pallidus. Furthermore, recent physiological and anatomical data has shown that virtually all striatal neurons contain dopamine D1 and D2 receptors; incongruent with the idea that dopamine differentially affects the direct and indirect pathway via its effects upon these two receptors (Parent et al., 2000). Bischoff (1998) proposed that the BG are involved in two tasks: the inhibition of motor activity and the provision of next sensory state information to cortex. She suggested that the indirect pathway, composed by globus pallidus external segment (GPe), subthalamic nucleus (STN) and the putamen area related to preparatory activity, is responsible for movement inhibition and that the direct pathway, composed by globus pallidus internal segment (GPi) and the putamen area related to movement activity, is involved in the provision of next sensory state information. She tested her model with three different tasks: a conditional elbow flexion/extension movement in response to the presence of a target shown to a rhesus monkey; a reciprocal aiming task loop in which subjects must tap a stylus between two targets in an alternating fashion as fast as possible; and a sequencing task where monkeys were trained to perform a push, pull or turn of a manipulandum in four different sequence orders. These tasks could serve as basic building blocks to create complex motor programs, but she didn’t explain how such building blocks could be linked in order to form complex motor programs. She needed three different models of the supplementary motor area (SMA), an area often linked to sequential behavior (Tanji, 2001; Jäncke et al., 2000; Hikosaka et al., 1998) and higher order planning or preprogramming (Humphrey and Tanji, 1991), to accommodate the needs of each type of task. We built a model that, based on Parent and colleagues’ recent neuroanatomical findings, incorporates the capability to manage complex motor sequences using a single SMA model for all type of tasks, and the possibility to learn novel action chains, reusing previous knowledge. We don’t have anymore a clear differentiation between the direct and indirect pathways, in fact we have a motor inhibition module and a “competing-movements” working memory that allows the recursive unfolding of sequence behavior.



Mármol Yahya and Arbib's BG model functional architecture.

In our new model, the putamen neurons involved in the preparation of movement (PutNext) are the ones in charge of predicting the next states in the action chain based on a gradient disinhibition. SMA is a self-organized map (Araújo and Barreto, 2002) that contains a set of motor sub-sequences. We adapted Amari's (1972) temporal associative memory concept to store in cortico-striatal weights the sequences of motor programs. This prediction is temporarily stored in a working memory loop. The neuron with the highest activation is selected and sent to GPi. STN has two roles; the first one is in charge of the inhibition of the ongoing sequence, while the second one is in charge of inhibiting the competing motor programs. The first inhibition is released when the preparatory activity decreases in SMAPropPrep. The second inhibition is released when a corollary discharge coming from the movement related neurons in the putamen (PutMvt) erases this action from the working memory, allowing the execution of the rest of the sequence. When the predicted movement is sent to cortex through thalamus, the SMAPropPrep would send the piece of the sequence previously predicted to the putamen neurons in charge of the preparation of movement. This will predict a new piece of the sequence, and the cycle starts again. It's important to mention that we are modeling the up-down state behavior of putamen neurons. Only if there is significant amount of coincident input in the putamen, it will fire. This is important since the corollary discharge is not sent until we know that this piece of the sequence is not longer needed. This system works as a finite state automaton. This allows us not only to unfold the sequences stored in cortex, but also to parse perceived sequences. The model successfully replicated the behaviors proposed by Bischoff (1998) using just one SMA model for all the tasks. It also successfully simulated some of the behaviors present in Parkinson's disease patients, by adding the interaction between the substantia nigra pars compacta and STN.