Using contraction analysis to design a model of the cortico-baso-thalamo-cortical loops

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The basal ganglia (BG) are a set of interconnected subcortical nuclei (detailed in Fig. 1) present in all vertebrates. They are thought to constitute a generic selection circuit, interacting with various cortical and subcortical systems involved in sensorimotor, cognitive or limbic processes. The interaction of the BG with the cortex takes place in parallel cortico-baso-thalamo-cortical (CBGTC) loops (Alexander et al., 1986).

Depending on the involved circuits, the role of the BG can be to select the most appropriate behaviour in a given context, the target of a saccade among the multiple points of interest present in the visual field, the piece of information to be stored in working memory, etc. Each of these elements competing for selection is represented by a channel inside the BG. The selection mechanism is disinhibition (Chevalier and Deniau, 1990). At rest, the output of the BG tonically inhibits the circuits enabling the activation of the competing elements. When one of them wins the competition, the inhibitory output of the corresponding channel is removed and the target circuit can be activated.

Numerous computational models of the basal ganglia have been proposed in the last ten years (Gillies and Arbruthnott, 2000, for a review). However most of them rely on the outdated "direct/indirect pathways" scheme proposed by Albin et al. (1995), which doesn't take into account numerous connections. Even the latest and most complete ones (Gurney et al., 2001; Frank et al., 2000) neglect some interesting projections. Moreover, despite the fact that the cortico-baso-thalamic circuitry contains numerous internal loops susceptible to generate various dynamic behaviours, the model's dynamics was not analysed.

Consequently, we propose a new model of the cortico-baso-thalamo-cortical loops including usually neglected connections and prove the stability of its operation using contraction analysis (Lohmiller and Slotine, 1998). Contraction analysis is an extension to nonlinear systems of the stability analysis for linear systems. It is well adapted to study the dynamics of artificial neural networks made of nonlinear components. Moreover, contraction has the advantage of being preserved through basic system combinations (hierarchies, feedback, etc.).

The details of the basal ganglia part of our model were previously presented (Girard et al., 2005) (see Fig. 1, Basal Ganglia dashed box). In accordance to neurobiological data (Parent et al., 2000; Kita et al., 1999), it includes projections from the external globus pallidus (GPe) to the striatum, which are usually neglected, moreover the projections from the GPe to the subthalamic nucleus (STN), the internal globus pallidus (GPi) and the substantia nigra pars reticulata (SNr) are considered diffuse. It was proved to be contracting and to perform efficient selection. Given known thalamus anatomy and relationships with cortex and basal ganglia (Pinault, 2004), we add a simple thalamo-cortical module to the existing BG model (see Fig. 1, Thalamus and cortex dashed boxes) in order to close the loop. The module itself is contracting and thanks to contraction combination properties, the proof of the contraction of the resulting circuit is very simple.

Depending on the CBGTC loop considered, the thalamic nuclei involved (ventro-lateral, medio-dorsal, etc.), as well as the sensory and frontal cortical areas, may vary. They are respectively represented by the TH nucleus and the SCtx and FCtx areas in Fig. 1. The excitatory TH-FC loop is proposed to have a role of amplification of the sensory signal, it is however under the inhibitory control of the thalamic reticular nucleus (TRN). Thus, as projection weights are constrained so that the module is contracting, it is proved that the activity in the loop cannot saturate and self-sustain indefinitely. The system thus avoids getting locked in a given state, which would not subsequently be influenced by any changes in the external input.

The basal ganglia inhibitory input to the thalamus selectively controls the amplification process: only the selected channel is amplified, while the low level signal in the other channels is preserved as the BG don't inhibit the cortex directly. Consequently, even if the signal corresponding to the winning channel only reaches the subcortical targets of the BG, the whole information is kept in the cortex.

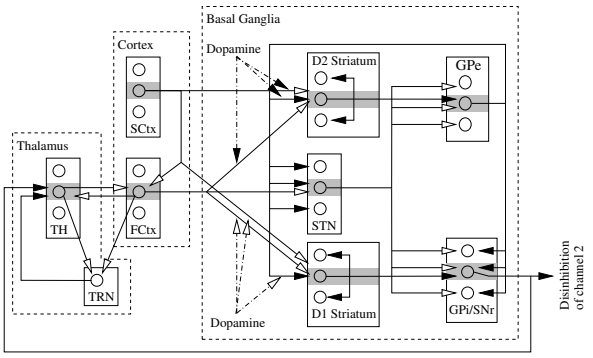

Figure 1: Cortico-baso-thalamo-cortical loop model with three competing channels represented (second channel shaded). Projections from the second channel neurons only are represented. Boxes : subcortical nuclei or cortical areas; circles: artificial leaky-integrator neurons; white arrowheads: excitatoty projections; black arrowheads: inhibitory projections; D1 and D2: neurons of the striatum with two respective types of dopamine receptors; STN: subthalamic nucleus; GPe: external segment of the globus pallidus; GPi/SNr: internal segment of the globus pallidus and substantia nigra pars reticulata; TH: thalamic nucleus (depends on the loop considered); TRN: thalamic reticular nucleus; FCtx: Frontal cortical area involved in the loop; SCtx: Sensory cortex providing the external input to the circuit. Dopamine level has a modulatory effect on the striatal input.

Concerning neuromimetism, the model proposed still omits two BG nuclei projections, from the STN to the striatum D1 and D2 (Parent et al., 2000) and from the D1 striatum neurons to the GPe (Wu et al., 2000). The STN neurons projecting to the striatum constitute a population distinct from those projecting to the GPe, GPi and SNr. We plan to investigate the possible role of such a specific interconnection in future versions of the model. The D1-GPe projection could improve the quality of the selection, as it did for the Gurney *et al.* model (Gurney et al., 2004), nevertheless, this adds an new loop whose contraction must be assessed. Finally, the inhibitory interneurons of the striatum were not modelled and might also add some selectivity.

This model is a part of a larger work aiming at modelling interactions of the various cortical and subcortical components of the saccadic circuitry. For this purpose, we designed a contracting superior colliculus/brainstem saccade burst generator model (unpublished yet). As the basal ganglia also form loops with the superior colliculus (McHaffie et al., 2005), future work will aim at connecting the two models, using contraction analysis to simply address the dynamics of the resulting intricate loops.

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