A Natural History of Skills

ABSTRACT. The dorsal pallium (a.k.a. the cortex in the mammals) makes a large loop circuit with the basal ganglia and the thalamus known to control and adapt behavior but the who's who of the functional roles of these structures is still debated. Influenced by the Triune brain theory that was proposed in the early sixties, many current theories propose a hierarchical organization on the top of which stands the cortex to which the subcortical structures are subordinated. In particular, habits formation has been proposed to reflect a switch from conscious on-line control of behavior by the cortex, to a fully automated subcortical control.**We propose instead to revalue the function of the network in light of the current experimental evidence concerning the anatomy and**

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HIGHLIGHTS

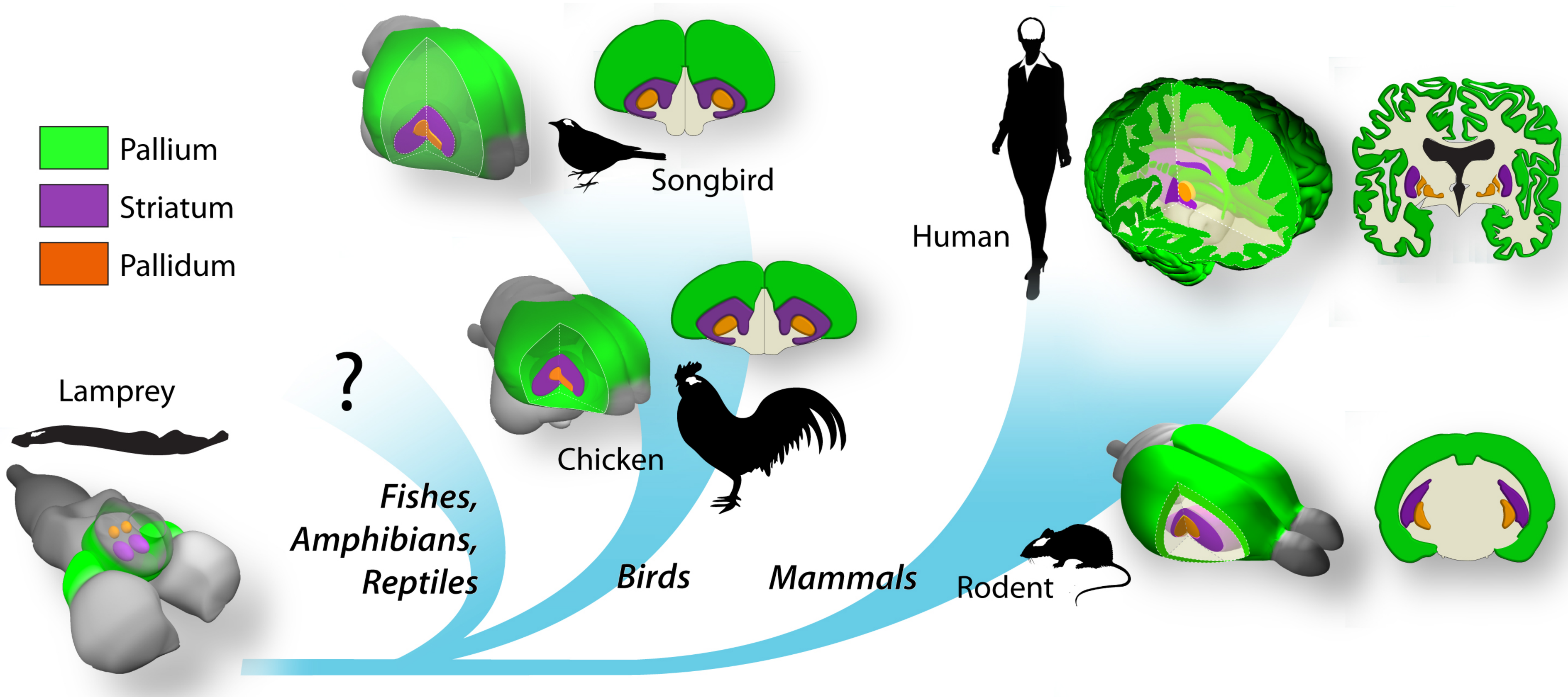
We revalue the function of the CBG loop in light of the evolution of the circuits in vertebrates.

We review the current theories and show that they could be merged in a broader framework of skill learning and performance.

We lay out the hypothesis that the development of automatized skills relies on the BG teaching cortical circuits.

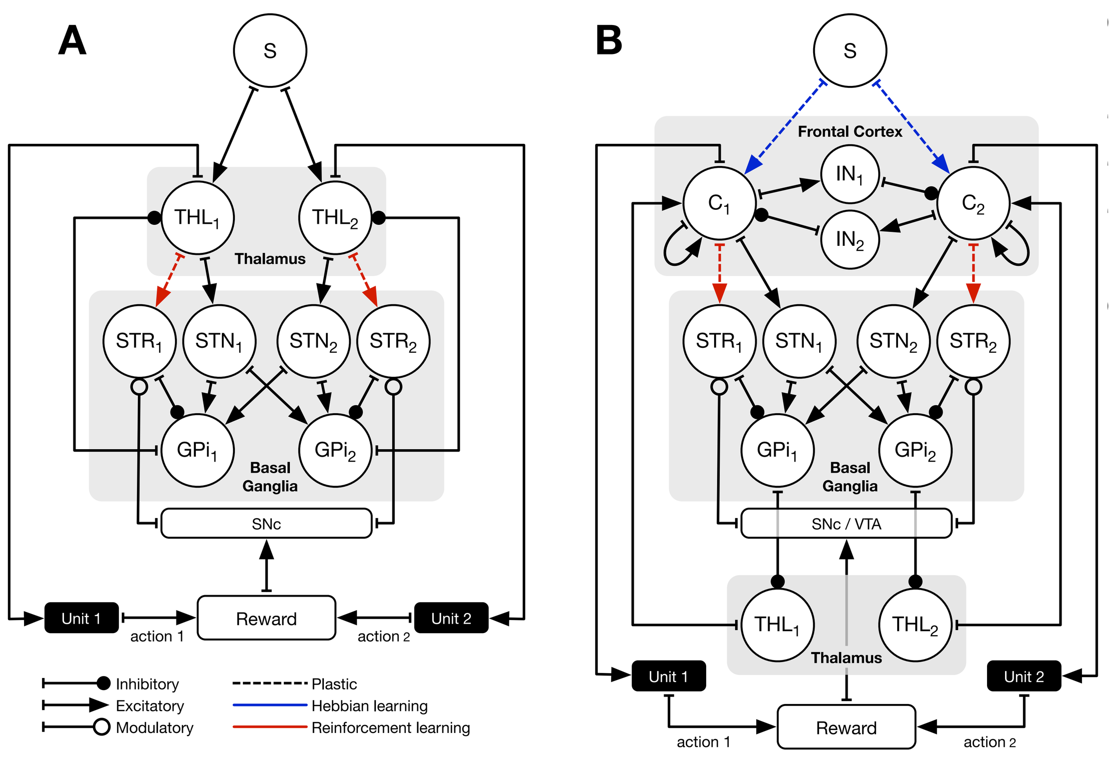
We show that it is linked with the development of a specialized dorsal pallium that evolved in parallel in different taxa.

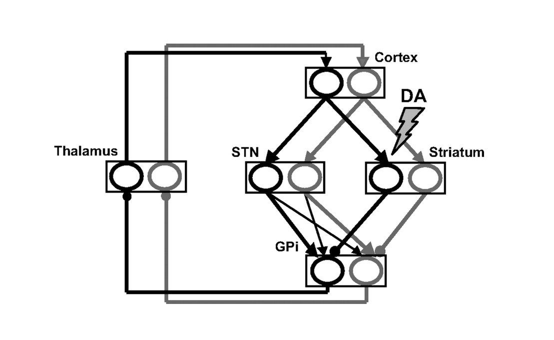
We conclude with a minimal computational framework where this hypothesis can be explicitly implemented and tested.



The frontal cortex, the basal ganglia (BG) and the thalamus are associated into a tripartite functional loop known as the cortex-basal ganglia loop (CBG loop). Since the early 90s, we roughly subdivide this broad network into 3 subparts, from the central sulcus to the frontal pole: a motor loop, a cognitive loop and a limbic loop. This terminology has been coined by human/primate anatomists, physiologists and clinicians according to the functions associated to the corresponding cortical area. The motor loop (a.k.a. the extrapyramidal loop for the anatomists) drives voluntary movement and learning, the cognitive loop performs planning and decision making, while the limbic loop is in charge of emotions and mood. Despite different functional roles, the similarities in the architecture of these loops bring to the idea that they share the same dynamical properties and process neural information along similar mechanisms. However, if everybody agreed that these processes lie ultimately upon a focal activation of a specific cortical area that triggers an action/decision/emotion (at least in primates), there are many discrepancies in the literature about the who's who (what's what?) of the relationship between neural substrate and functions.

The question is insidiously overshadowed by the triune brain theory proposed by Paul D. MacLean in the 1970s. Briefly, this theory assumes that the brain evolved in three stages, each of them adding new behavioral features to the ethogram (the inventory of behaviors) of the species granted with this upgrade. At first, appeared a reptilian brain (grossly the diencephalon and the BG) that brings instinctual behaviors (aggression, dominance, territoriality, ritual displays, etc.). Then, the paleo-mammalian complex (limbic system) involved in feeding, reproductive and parental behaviors in animals granted with the ability to display motivation and emotion. Finally, species at the top of the evolutionary tree were gifted with a neo-mammalian brain that allowed them to perform abstract thinking, planning, and for the most advanced of them language. Each level inhibited the lower one and the key to human neuropsychiatric pathology stems from defects in these inhibition processes. The triune brain theory was widely diffused because of its elegant adequacy between structure and function and vague similarities with Freud's psychoanalysis theories. It became familiar to a broad popular audience thanks to authors such as Carl Sagan or Arthur Koestler. Even if **the triune brain theory is long considered as outdated**, it is still influential in psychology. For our concern, it influenced the neurobiology of decision making, by establishing 3 dogmas: i) there is a hierarchical classification of higher brain functions; ii) each function is underlain by a specific anatomic structure and iii) structures compete against each other in order to produce a behavior. All the theories that have been proposed to explicit





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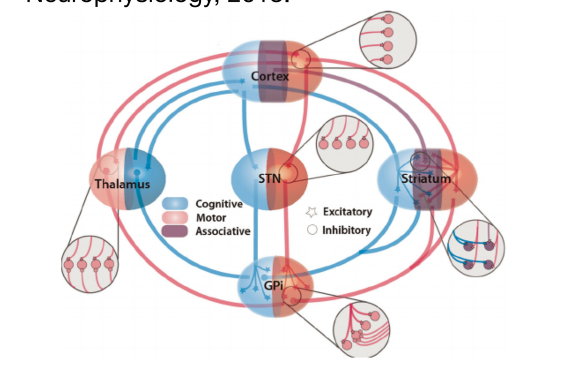

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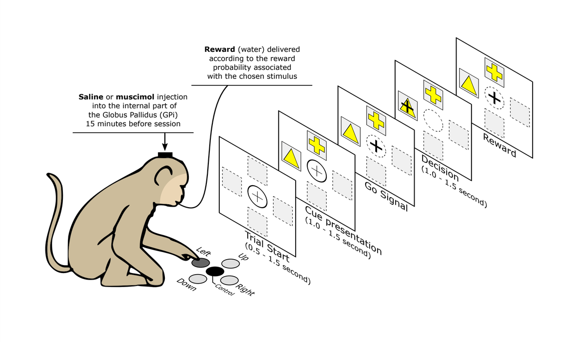

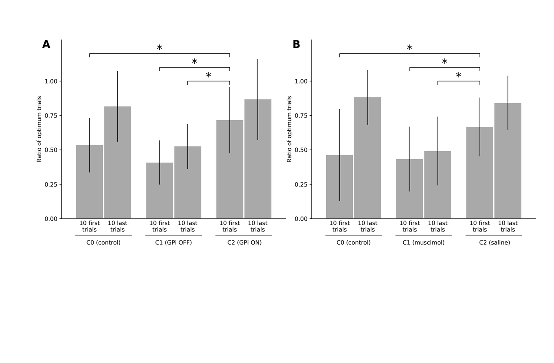

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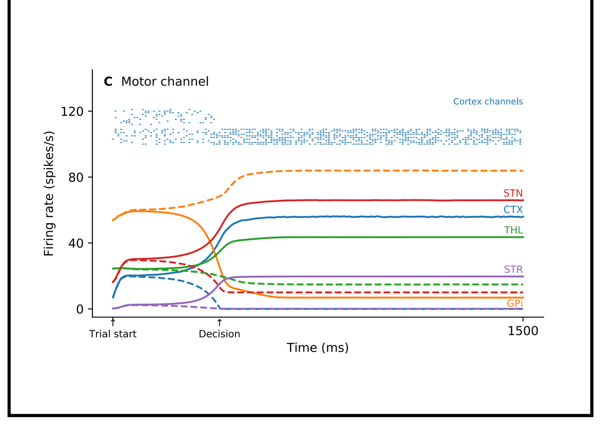

We think that adopting a phylogenetic approach to the decision-making network helps to explain how it works in the species with the most complex brains, such as primates. In this taxonomic order, our conclusions are very close to the Speed theory that states that the BG acting as "a general training machine for cortico-cortical connections". However, we show that it accounts for a late phase of the evolution that appeared in parallel in mammals and birds and maybe some fishes that are able to develop automatic skills. In other species, subcortical loops drive most of the behavior and therefore even if they are capable of RL driven flexibility, they lack the capacity to develop strong automatic skills in order to optimize their performance.

The phylogenetic approach to understanding decision making is still in its infancy. We should gather information more comprehensively in lower vertebrates (fishes, amphibians, reptiles), mammals and birds in order to test our theory. For example, it has been demonstrated that salamanders, an amphibian with a brain architecture close to that of the lamprey, can be trained to perform a navigation task. We just started an experimental study to test whether it relies on a classical DA dependent RL process and if we can operationalize habitual behavior in these species (according to our hypothesis, we should not).

Finally, this theory provides an anatomical support to the think fast-think slow theory developed by Kahneman. He proposed that human decision making is the result of a competition between a fast, automatic system that is prone to make mistakes and a slower, more demanding system that is more reliable. Kahneman himself never identified a neuroanatomical substrate of his theory, but many others have tried to put it in parallel with a triune brain organization: the fast system being associated to the “reptilian brain”, while the slow one is identified as a product of the “neo-mammalian cortex”. In fact, our proposition takes the opposite line. **According to us, the slow system is the older RL dependent cortico-subcortical loop, while the fast one results from cortical Hebbian**