
THE FUNCTIONAL ROLE OF THE STRIATUM AS AN ACTION EVALUATION CIRCUIT: A NETWORK-LEVEL THEORY

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ABSTRACT

Action selection is important for species survival. The basal ganglia, a subcortical structure, has long been thought to play a crucial role in action selection and movement initiation. Classical theories suggest that an important role of the striatum, the input region of the basal ganglia, is to select actions to be performed based on cortical projections carrying action information. However, thanks to recent progress in neural recording techniques, new experimental evidence suggests that the striatum does not perform action selection. Rather, the striatum plays an advisory role. Thus the classical theories of the basal ganglia need to be revisited and revised. As a first step, in this work we hypothesize a new computational role for the striatum. We present a network-level theory in which the striatum transforms cortical action bids into action evaluations. Based on the region's neural circuitry, we theorize that the role of the striatum is to transform bids to action values that are normalized, contrast-enhanced, orthogonalized, and encoded as continuous values through the use of two separate neuron populations with bipolar tuning and both feedforward and collateral inhibitory mechanisms. We simulate our network and investigate the role of the network components in its dynamics. Finally, we compare the behavior of our network to previous literature on decision-making behavior in rodents and primates.

1 Introduction

Accurate reward and cost evaluation of available behavioral actions is a process necessary for species survival. The basal ganglia (BG), a subcortical structure, is thought to play a critical role in such action selection and long term behavioral tuning. The BG receives topographically organized projections from nearly all areas of cortex along with projections from the thalamus, hippocampus, and amygdala. BG inputs are organized into two clear pathways called the “go” (also called direct or D1) and “no-go” (also called indirect or D2) pathways which are thought to promote and suppress the selection of motor behaviors. The output of the D1 and D2 pathways project back to cortex through the thalamus, forming parallel loops [Foster et al., 2021, Fang and Creed, 2024, Shipp, 2017].

Despite this detailed anatomical understanding and extensive experimental research, the field has yet to formulate a theory that adequately encompasses all recognized aspects of BG functionality. The BG is a complicated circuit which influences behavior in many ways, making the challenge of formulating any reasonable theory very difficult. A long standing network-level theory has existed on the role of the BG and the D1-D2 pathways. In this classical theory the striatum, the input layer to the basal ganglia, ultimately selects the optimal behavioral action by exciting cortex through its direct pathway projections and inhibiting cortical activity of all other competing actions through its indirect pathway projections [Berns and Sejnowski, 1996, Mink, 1996, Hikosaka et al., 2000]. The winning action is assumed to be executed through neurons in the motor cortex.

The classical BG theory has been longstanding. However, recent advances in neural recording techniques have lead to new experimental evidence that suggests a need for a revised theory of the BG’s role in action selection and decision-making. A new picture is developing in which the striatum does not directly select actions or control motor output. Instead the striatum seems to signal the salience of all available actions for the task at hand [Cox and Witten, 2019]. Further, these salience signals seem to be modulated by state variables, either internal or from the external environment Bolkan et al. [2022], Shipp [2017].

We propose that the first step to updating the classical BG theory is to develop a network-level striatal theory that is informed by the detailed neurobiology of the region and newly emerging experimental evidence. In this work we present such a theory, suggesting a new role for the striatum in decision-making. We hypothesize that the role of the striatum is to perform action evaluation instead of action selection, where action evaluation is done through normalization, orthogonalization, and contrast enhancement of competing action information from cortical inputs. Our theoretical ideas are informed by the detailed neurobiology of the region, which is similar in architecture to popular normalization networks such as shunting inhibition networks and recurrent competitive fields [Chandler and Grossberg, 2012, Grossberg, 1982]. We implement our striatal network in simulation, and remarkably, we find that our network reproduces the experimental results of behavioral decision-making in rodents and humans.

In summary the contributions of this work are: (1) We hypothesize a new computational perspective of the striatum (the input region to the BG) as a action evaluation circuit instead of an action selection circuit, where action evaluations are normalized and encoded on orthogonal manifolds in neuronal activity space by bipolar neuron populations. (2) We present a network-level striatal theory of our hypothesis that captures the well known neurobiology of the region and the new experimental evidence. (3) We implement our network theory; through simulation we investigate the roles of the network components and qualitatively compare the behavior of the network to action selection of rodents and humans.

2 Anatomy of the cortico-striatal circuit

The output neurons of the striatum are the spiny projection neurons (SPNs). These neurons are also the principle neuron type, with over 95% of the neurons within the striatum being SPNs [Gerfen and Surmeier, 2011]. SPN neurons integrate information from thousands of excitatory upstream cortical neurons and project to downstream BG nuclei. SPNs are inhibitory neurons, inhibiting not only downstream targets but also SPNs within the striatum through collateral connections [Plenz and Wickens, 2016]. There are two equally sized subpopulations of striatal SPN neurons: dSPN neurons, which are direct pathway (D1) projecting, and iSPN neurons, which are indirect pathway (D2) projecting. Further, dSPN and iSPN neurons are oppositely modulated by dopamine inputs. An increase in dopamine increases (decreases) the excitability of dSPN (iSPN) neurons and a decrease in dopamine has the opposite effect [Maltese et al., 2021, Prager et al., 2020, Tritsch and Sabatini, 2012].

A second principle neuron type in the striatum are the parvalbumin (PV)-expressing fast spiking interneurons. These inhibitory neurons make up 1% of the striatum. They receive the same cortical projections as SPNs and directly inhibit the same SPNs, thus implementing a feedforward inhibitory motif. PV neurons have been shown to have a divisive normalization network effect in vivo [Wilson et al., 2012]. There exists other inhibitory interneuron types within the striatum but their connectivity and functions are less studied.

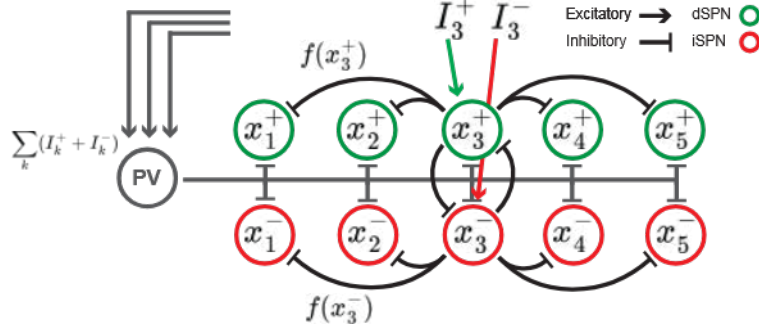


Figure 1: Diagram of our cortico-striatal neural network for a 5-action scenario. For clarity, input and collateral SPN connections are shown only for the third action, but connections are consistent across all SPNs.

Lastly, the striatum has a compartment-level organization. There are two compartments: striosomes and matrix, where the matrix compartment makes up $> 85\%$ of the striatum [Friedman et al., 2020]. The matrix compartment projects to the above discussed direct and indirect pathways, whereas the smaller striosomal compartment projects to midbrain dopamine containing neurons [Crittenden et al., 2016, Evans et al., 2020, Hong and Hikosaka, 2013, Hong et al., 2019]. In this work, we focus on the matrix compartment of the striatum. However, because SPN collaterals do not cross compartment (striosomes and matrix) boundaries – meaning striosomal-SPNs and matrix-SPNs do not directly communicate – we believe that our theoretical motifs will generally hold across compartments, and we leave adapting our motifs presented in this work to striosomes as future work.

3 A network-level theory of striatal action evaluation

We present a revised network-level theory for the role of the striatum as an action evaluation circuit for planning and decision-making. Here we use the term ‘action’ for convenience, but we allow the meaning of action to extend beyond behavior to events of cognition and emotional states. Our theory makes three algorithmic predictions: (1) Action values have bipolar encodings where dSPN activity encodes positive evaluation of the action and iSPN activity encodes negative evaluation of the action. The encodings for differing actions lie on orthogonal manifolds in neuronal activity space. Such an organization allows for precise modulation of specific actions and continual learning through dopamine innervations [Ajemian et al., 2013, French, 1999, Liu et al., 2021]. (2) Cortico-striatal feedforward inhibition implements input normalization for output gain control. Normalization has computational benefits such as maximizing neuron sensitivity and facilitating the discrimination of input representations. (3) Intralayer SPN collateral connections enhance the contrast of network outputs through competitive inhibition. Together these components produce a neural circuit that transforms cortical variables pertaining to action into competing bids for action selection.

Let there be K possible actions. Our network will have K dSPN neurons and K iSPN neurons. SPN neuron dynamics follow a shunting inhibition neuron model [Grossberg, 1982, Chandler and Grossberg, 2012] with unbalanced collateral inhibition:

$$\begin{aligned} \frac{dx_i^+}{dt} &= -Ax_i^+ + (B - x_i^+)I_i^+ - x_i^+ \left(\sum_k (I_k^+ + I_k^-) + \sum_{k \neq i} f(x_k^+) + f(x_i^-) \right) \\ \frac{dx_i^-}{dt} &= -Ax_i^- + (B - x_i^-)I_i^- - x_i^- \left(\sum_k (I_k^+ + I_k^-) + \sum_{k \neq i} f(x_k^-) + f(x_i^+) \right) \end{aligned}$$

The variables x_i^+ and x_i^- are the activities of the dSPN and iSPN neurons representing the i th action, respectively. A is the passive decay rate of the cell membrane. I_i^+ and I_i^- are nonnegative continuous valued positive and negative action salience inputs from cortex, and B is the excitatory saturation point of the cell. Inhibition comes in the form of feedforward inhibition from a single PV neuron, modeled as the summation $\sum_k (I_k^+ + I_k^-)$, and imbalanced collateral inhibition [Burke et al., 2017], $\sum_{k \neq i} f(x_k^+) + f(x_i^-)$ or $\sum_{k \neq i} f(x_k^-) + f(x_i^+)$ where the signal feedback function is $f(z) = \frac{z^2}{0.5 + z^2}$. See Figure 1 for a diagram of the network where $K = 5$.

At steady state this network implements a form of divisive normalization. Divisive normalization is common neural motif found in the activity of many brain regions such as vision [Carandini and Heeger, 2012, Grossberg, 1982] and olfaction [Olsen et al., 2010], as well as at the behavioral level in action selection [Louie et al., 2013].

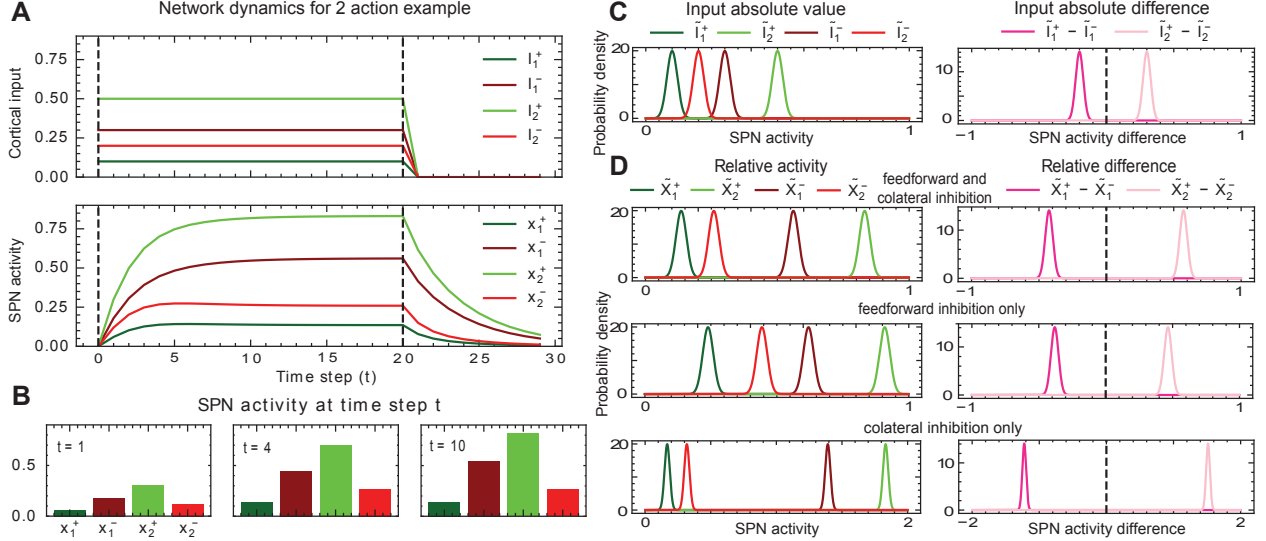


Figure 2: Network dynamics for a 2-action example. (A) Network inputs (top) and network SPN activity (bottom) over time. (B) Snapshots of SPN activity in A at specified timesteps. (C) Input values with added noise (left) and difference (right) at $t = 20$. (D) Network output with added noise at $t = 20$ for full network (top), network without collaterals (middle), and network without feedforward inhibition (bottom).

We implement a discrete time simulation of our network with parameters $A = .05$ and $B = 3$. We sometimes include constant output additive noise in our simulations, i.e., $\tilde{x}_i^+ = x_i^+ + \epsilon$ where $\epsilon \sim N(0, \sigma)$, and compare these noisy output representations to noisy input representations that do not pass through the model, i.e., $\tilde{I}_i^+ = I_i^+ + \epsilon$.

4 Results

Our cortico-striatal neural network implementation exhibited normalization and contrast enhancement dynamics and reproduced decision-making behavior of rodents and humans. We first explored the dynamics of the network for a 2-action scenario where $(I_1^+, I_1^-, I_2^+, I_2^-) = (0.1, 0.3, 0.5, 0.2)$ (Figures 2A and 2B). The network ran for 30 time steps where input was present for only the first 20 time steps. The network outputs (Figure 2A, bottom) enhanced the differences between the inputs while maintaining qualitative input information in a constrained activity range.

To investigate the importance of the different components of our network, we ran the same 2-action simulation with the addition of additive noise ($\sigma = 0.02$) on ablated networks. We compared the output activity at $t = 20$ of the ablated and complete networks to the network inputs with additive noise (Figure 2C). A network with only feedforward inhibition and no collateral connections normalized the input activities (Figure 2D, middle). Whereas a network with no feedforward inhibition and only collateral inhibition increased the contrast of output representations at the expense of increased overall network activity (Figure 2D, bottom). A network with both feedforward and collateral inhibition produced output representations with both of the desirable properties: contrast enhancement and constrained excitation (Figure 2D, top).

Behavioral level models of divisive normalization have explained primate action selection in both humans and monkeys [Louie et al., 2013]. We wondered if our network-level theory could also explain this behavior as well as explain rodent decision-making behavior in a task where the striatum has known involvement [Friedman et al., 2015]. We translate network output activity to behavior by taking the difference of sampled action values from the network output with additive noise, i.e., $\tilde{x}_i^+ - \tilde{x}_i^- \forall i$; the action with the most positive difference was the action whose behavior was performed.

We ran our network on a 2-action task (originally ran in rodents) where actions had both positive outcomes (in the form of chocolate milk) and negative outcomes (bright light). Based on the reward and cost present in each action, a task trial can be categorized as one of four possible categories of increasing conflict (i.e., the better choice is less obvious): non-conflict cost-benefit, benefit-benefit, cost-cost, and cost-benefit conflict (Figure 3A, adapted from Friedman et al. [2015]). Our network simulations (with $\sigma = .55$) reproduced the rodent experimental behavioral findings (Figure 3B, animal behavior adapted from Friedman et al. [2015]), and 3C, model behavior).

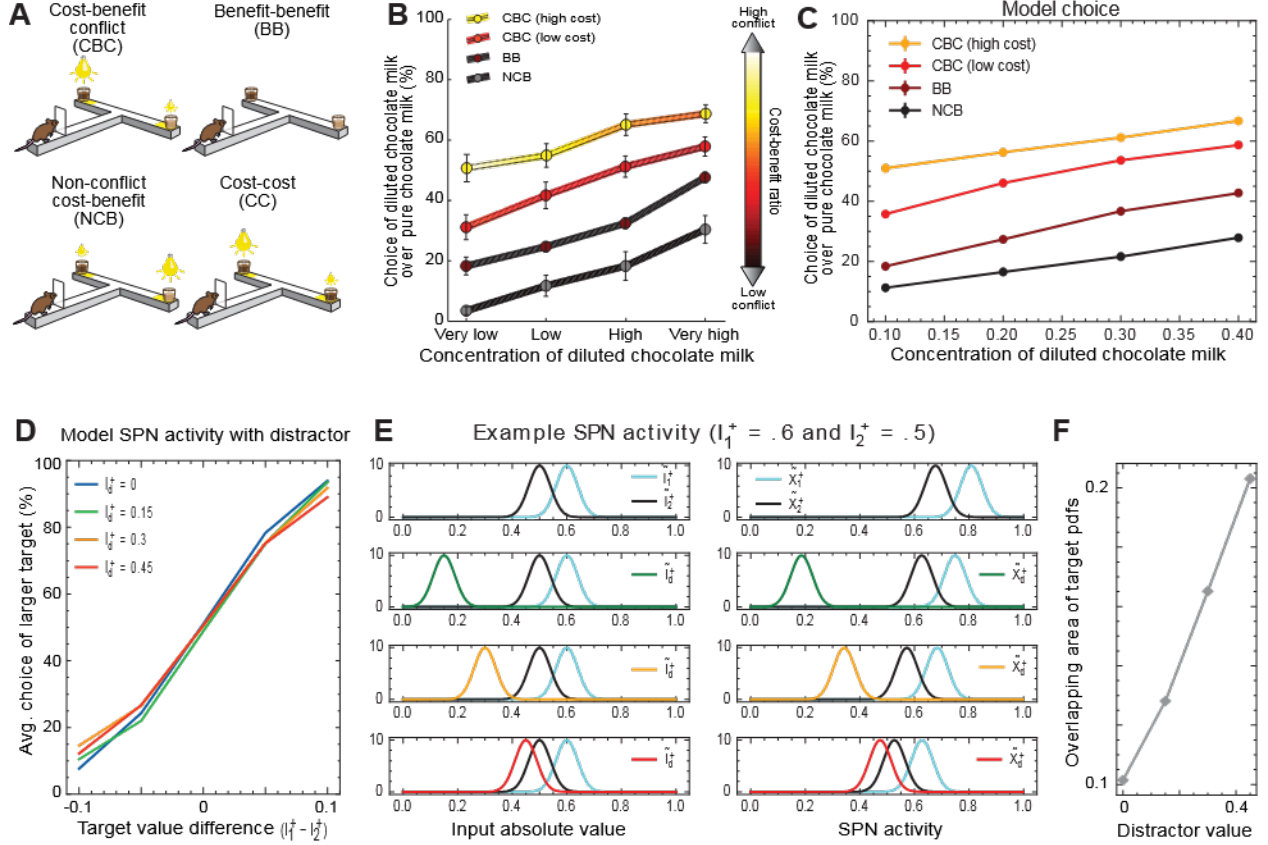


Figure 3: Comparison of network to animal experiments. (A) 2-choice task with four categories of conflicting choices (see Friedman et al. [2015]) (B) Rodent choice behavior. (C) Model choice behavior from network output activity. (D) Our network reproduces primate behavior in a 3-choice task where one choice is a distractor (see Louie et al. [2013]); I_d^+ is distractor choice value. (E) Network inputs with noise (left) and network outputs with noise (right) for example action values. (F) Distractor value impacts overlap of choice pdfs.

Louie et al. [2013] showed that action selection behavior in primates (both human and non-human) in a 3-action task, where one of the actions is a distractor action, can be explained by a behavioral-level model of divisive normalization. We reproduced their results using our neural network (with $\sigma = .04$). Note that the task had only positive value associations for each action, i.e., $I_i^- = 0 \forall i$. We reproduced their finding that the behavioral choice psychometric curve flattens as the value of the distractor, I_d^+ , increases (Figure 3D). This result could be explained by the increase in overlap of the SPN activity distributions of the available actions as the distractor value increased, due to network normalization mechanisms (Figure 3E and F).

5 Summary and Future Work

We are interested in revising the classical theory of the basal ganglia to account for the recent experimental evidence that has become available thanks to new neural recording techniques, such as calcium imaging. As a first step in this direction, in this work we proposed a new network-level theory of the striatum. We showed that the striatum may be another example of divisive normalization in the brain. Further, we proposed that the striatum's role is to not select actions as previously theorized, but instead to provide orthogonal bipolar representations of action values where dSPNs encode positive salience and iSPNs encode negative salience.

Future directions of this work include: (1) Adding dopamine as an SPN input to modulate action evaluation [Carandini and Heeger, 2012, Maltese et al., 2021, Bolkan et al., 2022]. (2) Learning the orthogonal representations and demonstrating the importance of collaterals for such learning [Von der Malsburg, 1973]. (3) Utilizing our network as a prediction tool in understanding collateral organization since very little experimental evidence exists on this topic.

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