

1 PERSPECTIVES

2 **Thalamocortical contribution to flexible learning in neural systems**

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6 **Keywords:** [Meta-learning; Credit assignment; Continual learning; Thalamocortical interactions; Basal ganglia; Thalamus]

**ABSTRACT**

7 Animal brains evolved to optimize behavior in dynamic environments, flexibly selecting actions that  
8 maximize future rewards in different contexts. A large body of experimental work indicates that such  
9 optimization changes the wiring of neural circuits, appropriately mapping environmental input onto  
10 behavioral outputs. A major unsolved scientific question is how optimal wiring adjustments, which must  
11 target the connections responsible for rewards, can be accomplished when the relation between sensory  
12 inputs, action taken, environmental context with rewards is ambiguous. The credit assignment problem  
13 can be categorized into context-independent *structural credit assignment* and context-dependent  
14 *continual learning*. In this perspective, we survey prior approaches to these two problems and advance  
15 the notion that the brain's specialized neural architectures provide efficient solutions. Within this  
16 framework, the thalamus with its cortical and basal ganglia interactions serves as a systems-level solution  
17 to credit assignment. Specifically, we propose that thalamocortical interaction is the locus of  
18 meta-learning where the thalamus provides cortical control functions that parametrize the cortical activity  
19 association space. By selecting among these control functions, the basal ganglia hierarchically guide  
20 thalamocortical plasticity across two timescales to enable meta-learning. The faster timescale establishes

21 contextual associations to enable behavioral flexibility while the slower one enables generalization to  
22 new contexts.

## AUTHOR SUMMARY

23 Deep learning has shown great promise over the last decades allowing artificial neural networks to solve  
24 difficult tasks. The key to success is the optimization process by which task errors are translated to  
25 connectivity patterns. A major unsolved question is how the brain optimally adjusts the wiring of neural  
26 circuits to minimize task error analogously. In our perspective, we advance the notion that the brain's  
27 specialized architecture is part of the solution and spell out a path towards its theoretical, computational  
28 and experimental testing. Specifically, we propose the interaction between the cortex, thalamus and basal  
29 ganglia induces plasticity in two timescales to enable flexible behaviors. The faster timescale establishes  
30 contextual associations to enable behavioral flexibility while the slower one enables generalization to  
31 new contexts.

## INTRODUCTION

32 Learning to flexibly choose appropriate actions in uncertain environments is a hallmark of  
33 intelligence Miller and Cohen (2001); Niv (2009); Thorndike (2017). When animals explore unfamiliar  
34 environments, they tend to reinforce actions that lead to unexpected rewards. A common notion in  
35 contemporary neuroscience is that such behavioral reinforcement emerges from changes in synaptic  
36 connectivity, where synapses that contribute to the unexpected reward are strengthened Abbott and  
37 Nelson (2000); Bliss and Lomo (1973); Dayan and Abbott (2005); Hebb (2002); Whittington and Bogacz  
38 (2019). A prominent model for connecting synaptic to behavioral reinforcement is dopaminergic  
39 innervation of basal ganglia (BG), where dopamine (DA) carries the **reward prediction error** (RPE)  
40 signals to guide synaptic learning Bamford, Wightman, and Sulzer (2018); Bayer and Glimcher (2005);  
41 Montague, Dayan, and Sejnowski (1996); Schultz, Dayan, and Montague (1997). This circuit motif is  
42 thought to implement a basic form of the reinforcement learning (RL) algorithm Houk, Davis, and Beiser  
43 (1994); Morris, Nevet, Arkadir, Vaadia, and Bergman (2006); Roesch, Calu, and Schoenbaum (2007);  
44 Suri and Schultz (1999); R. Sutton and Barto (2018); R. S. Sutton and Barto (1990); Wickens and Kotter

45 (1994), which has had much success in explaining simple Pavlovian and instrumental  
46 conditioning Ikemoto and Panksepp (1999); Niv (2009); R. Sutton and Barto (2018); R. S. Sutton and  
47 Barto (1990). However, it is unclear how this circuit can reinforce the appropriate connections in  
48 complex natural environments where animals need to dynamically map sensory inputs to different action  
49 in a context-dependent way. If one naively credits all synapses with the RPE signals, the learning will be  
50 highly inefficient since different cues, contexts and actions contribute to the RPE signals differently. To  
51 properly credit the cues, context and actions that lead to unexpected reward is a challenging problem,  
52 known as the **credit assignment** problem Lillicrap, Santoro, Marris, Akerman, and Hinton (2020);  
53 Minsky (1961); Rumelhart, Hinton, and Williams (1986); Whittington and Bogacz (2019).

54 One can roughly categorize the credit assignment into context-independent *structural credit*  
55 *assignment* and context-dependent *continual learning*. In structural credit assignment, animals may  
56 make decisions in a multi-cue environment and should be able to credit those cues that contribute to the  
57 rewarding outcome. Similarly, if actions are being chosen based on internal decision variables, then the  
58 underlying activity states must also be reinforced. In such cases, neurons that are selective to external  
59 cues or internal latent variables need to adjust their downstream connectivity based on its contribution of  
60 their downstream targets to the RPE. This is a challenging computation to implement because, for  
61 upstream neurons, the RPE will be dependent on downstream neurons that are several connections away.  
62 For example, a sensory neuron needs to know the action chosen in the motor cortex to selectively credit  
63 the sensory synapses that contribute to the action. In *continual learning*, animals not only need to  
64 appropriately credit the sensory cues and actions that lead to the reward but also need to credit the  
65 sensorimotor combination in the right context to retain the behaviors learned from different contexts and  
66 even to generalize to novel contexts. Therefore, animals can continually learn and generalize across  
67 different contexts while retaining behaviors in familiar contexts. For example, when one is in the United  
68 States, one learns to first look left before crossing the street, whereas, in the United Kingdom, one learns  
69 to look right instead. However, after spending time in the UK, someone from the US should not unlearn  
70 the behavior of looking left first when they return home because their brain ought to properly assign the  
71 credit to a different context. Furthermore, once one learns how to cross the street in the US, it is much  
72 easier to learn how to cross the street in the UK because the brain flexibly generalize behaviors across  
73 contexts.

74 In this perspective, we will first go over common approaches from machine learning to tackle these  
 75 two credit assignment problems. In doing so, we highlight the challenge in their efficient implementation  
 76 within biological neural circuits. We also highlight some recent proposals that advance the notion of  
 77 specialized neural hardware that approximate more general solutions for credit assignment Fiete and  
 78 Seung (2006); Ketz, Morkonda, and O'Reilly (2013); Kornfeld et al. (2020); Kusmierz, Isomura, and  
 79 Toyozumi (2017); Lillicrap, Cownden, Tweed, and Akerman (2016); Liu, Smith, Mihalas, Shea-Brown,  
 80 and Sümbül (2020); O'Reilly (1996); O'Reilly, Russin, Zolfaghar, and Rohrlich (2021); Richards and  
 81 Lillicrap (2019); Roelfsema and Holtmaat (2018); Roelfsema and van Ooyen (2005); Sacramento,  
 82 Ponte Costa, Bengio, and Senn (2018); Schiess, Urbanczik, and Senn (2016); Zenke and Ganguli (2018).  
 83 Along these lines, we propose an efficient systems-level solution involving the thalamus and its  
 84 interaction with the cortex and BG for these two credit assignment problems.

## COMMON MACHINE LEARNING APPROACHES TO CREDIT ASSIGNMENT

85 One solution to structural credit assignment in machine learning is **backpropagation** Rumelhart et al.  
 86 (1986). Backpropagation recursively computes the vector-valued error signal for synapses based on their  
 87 contribution to the error signal. There is much empirical success of backpropagation in surpassing human  
 88 performance in supervised learning such as image recognition He, Zhang, Ren, and Sun (2016);  
 89 Krizhevsky, Sutskever, and Hinton (2012) and reinforcement learning such as playing the game of Go  
 90 and Atari Mnih et al. (2015); Schrittwieser et al. (2020); Silver et al. (2016, 2017). Additionally,  
 91 comparing artificial networks trained with backpropagation to neural responses from the ventral visual  
 92 stream of non-human primates shows comparable internal representations Cadieu et al. (2014); Yamins et  
 93 al. (2014). Despite its empirical success in superhuman level performance and matching the internal  
 94 representation of actual brains, backpropagation may not be straightforward to implement in biological  
 95 neural circuits as we explain below.

In its most basic form, backpropagation requires symmetric connections between neurons (forward and backward connections). Mathematically, we can write down the backpropagation in Equation 1:

$$\delta W_i \propto \frac{\partial E}{\partial W_i} = e_i f'(a_{i-1})^\top \quad (1)$$

where

$$e_i = W_{i+1}^\top e_{i+1} \circ f'(a_i),$$

96  $E$  is the total error,  $e_i$  is the vector error at layer  $i$ ,  $W_i$  is the synaptic weight connecting layer  $i - 1$  to  
 97 layer  $i$  and  $f$  is the nonlinearity. Intuitively, this is saying that the change of synaptic weight  $W_i$  is  
 98 computed by a Hebbian learning rule between backpropagation error  $e_i$  and activity from last layer  
 99  $f(a_{i-1})$  while the backpropagation error is computed by backpropagating the error in the next layer  
 100 through symmetric feedback weights  $W_{i+1}^\top$ . Importantly, in this algorithm, error signals do not alter the  
 101 activity of neurons in the preceding layers and instead operate independently from the feedforward  
 102 activity. However, such arrangement is not observed in the brain; symmetric connections across neurons  
 103 are not a universal feature of circuit organization, and biological neurons may encode both feedforward  
 104 inputs and errors through changes in spike output (changes in activity) Crick (1989); Richards and  
 105 Lillicrap (2019). Therefore, it is hard to imagine how the basic form of backpropagation (symmetry and  
 106 error/activity separation) is physically implemented in the brain.

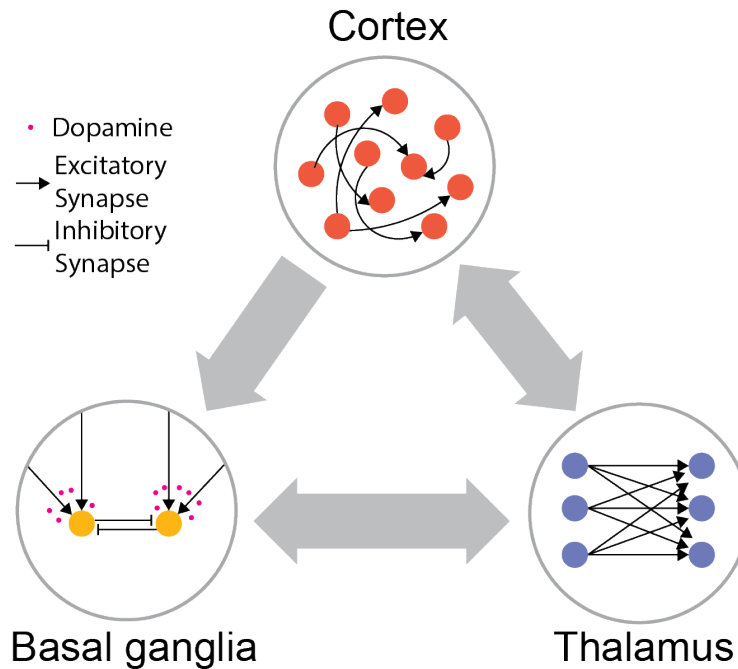
107 Furthermore, while an animal can continually learn to behave across different contexts, artificial neural  
 108 networks trained by backpropagation struggle to learn and remember different tasks in different contexts:  
 109 a problem known as **catastrophic forgetting** French (1999); Kemker, McClure, Abitino, Hayes, and  
 110 Kanan (2018); Kumaran, Hassabis, and McClelland (2016); McCloskey and Cohen (1989); Parisi,  
 111 Kemker, Part, Kanan, and Wermter (2019). Specifically, this problem occurs when the tasks are trained  
 112 sequentially because the weights optimized for former tasks will be modified to fit the later tasks. One of  
 113 the common solutions is to interleave the tasks from different contexts to jointly optimize performance  
 114 across contexts by using an episodic memory system and replay mechanism Kumaran et al. (2016);  
 115 McClelland, McNaughton, and O'Reilly (1995). This approach has received empirical success in  
 116 artificial neural networks including learning to play many Atari game Mnih et al. (2015); Schrittwieser et  
 117 al. (2020). However, since one needs to store past training data in memory to replay during learning, this  
 118 approach demands a high computational overhead and can be is inefficient as the number of the contexts  
 119 increases. On the other hand, humans and animals acquire diverse sensorimotor skills in different  
 120 contexts throughout their life span: a feat that cannot be solely explained by memory  
 121 replay M. M. Murray, Lewkowicz, Amedi, and Wallace (2016); Parisi et al. (2019); Power and Schlaggar

122 (2017); Zenke, Gerstner, and Ganguli (2017). Therefore, biological neural circuits are likely to employ  
123 other solutions to continual learning in addition to memory replay.

124 Therefore, to solve these two credit assignment problems in the brain, one needs to seek different  
125 solutions. One of the pitfalls of backpropagation is that it is a general algorithm that works on any  
126 architecture. However, actual brains are collections of specialized hardware put together in a specialized  
127 way. It can be conceived that through clever coordination between different cell types and different  
128 circuits, the brains can solve the credit assignment problem by leveraging its specialized architectures.  
129 Along this line of ideas, many investigators have proposed cellular Fiete and Seung (2006); Kornfeld et  
130 al. (2020); Kusmierz et al. (2017); Liu et al. (2020); Richards and Lillicrap (2019); Sacramento et al.  
131 (2018); Schiess et al. (2016) and circuit level mechanisms Lillicrap et al. (2016); O'Reilly (1996);  
132 Roelfsema and Holtmaat (2018); Roelfsema and van Ooyen (2005) to assign credit appropriately. In this  
133 perspective, we would like to advance the notion that the specialized hardware arrangement also happens  
134 at the system level and propose that the thalamus and its interaction with basal ganglia (BG) and the  
135 cortex serve as a system-level solution for these three types of credit assignment.

## **A PROPOSAL: THALAMOCORTICAL-BASAL GANGLIA INTERACTIONS ENABLE META-LEARNING TO SOLVE CREDIT ASSIGNMENT.**

139 To motivate the notion of thalamocortical-basal ganglia interactions being a potential solution for credit  
140 assignment, we will start with a brief introduction. The cortex, thalamus and basal ganglia are the three  
141 major components of the mammalian forebrain – the part of the brain to which high level cognitive  
142 capacities are attributed to Alexander, DeLong, and Strick (1986); Badre, Kayser, and D'Esposito (2010);  
143 Cox and Witten (2019); Makino, Hwang, Hedrick, and Komiyama (2016); Miller (2000); Miller and  
144 Cohen (2001); Niv (2009); Seo, Lee, and Averbeck (2012); Wolff and Vann (2019). Each of these  
145 components has its specialized internal architectures; the cortex is dominated by excitatory neurons with  
146 extensive lateral connectivity profiles Fuster (1997); Rakic (2009); Singer, Sejnowski, and Rakic (2019),  
147 the thalamus is grossly divided into different nuclei harboring mostly excitatory neurons devoid of lateral  
148 connections Harris et al. (2019); Jones (1985); Sherman and Guillery (2005), and the basal ganglia are a  
149 series of inhibitory structures driven by excitatory inputs from the cortex and thalamus Gerfen and Bolam  
150 (2010); Lanciego, Luquin, and Obeso (2012); Nambu (2011) (Figure 1). A popular view within system



136 **Figure 1. Distinct architectures of cortex, thalamus and basal ganglia** Cortex is largely composed of excitatory neurons with extensive recurrent connec-  
 137 tivity. Thalamus consists of mostly excitatory neurons without lateral connections. Basal ganglia consist of mostly inhibitory neurons driven by cortical and  
 138 thalamic inputs, and the corticostriatal plasticity is modulated by dopamine.

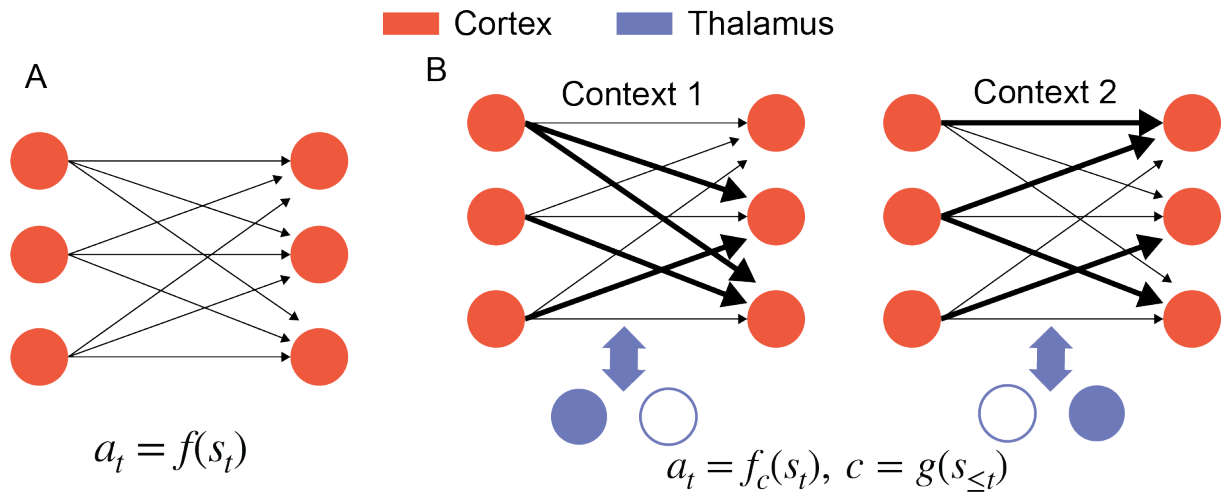
151 neuroscience stipulates that BG and the cortex underwent different learning paradigms where BG is  
 152 involved in reinforcement learning while the cortex is involved in unsupervised learning Doya (1999,  
 153 2000). Specifically, the input structure of the basal ganglia known as the striatum is thought to be where  
 154 reward gated plasticity takes place to implement reinforcement learning Bamford et al. (2018); Cox and  
 155 Witten (2019); Hikosaka, Kim, Yasuda, and Yamamoto (2014); Kornfeld et al. (2020); Niv (2009); Perrin  
 156 and Venance (2019). One such evidence is the high temporal precision of DA activity in the striatum. To  
 157 accurately attribute the action that leads to positive RPE, DA is released into the relevant corticostriatal  
 158 synapses. However, DA needs to disappear quickly to prevent the next stimulus-response combination  
 159 from being reinforced. In the striatum, this elimination process is carried out by dopamine active  
 160 transporter (DAT) to maintain a high temporal resolution of DA activity on a timescale of around  
 161 100ms-1s to support reinforcement learning Cass and Gerhardt (1995); Ciliax et al. (1995); Garris and  
 162 Wightman (1994). In contrast, although the cortex also has dopaminergic innervation, cortical DAT  
 163 expression is low and therefore DA levels may change at a timescale that is too slow to support

164 reinforcement learning Cass and Gerhardt (1995); Garris and Wightman (1994); Lapish, Kroener,  
165 Durstewitz, Lavin, and Seamans (2007); Seamans and Robbins (2010) but instead support other  
166 processes related to learning Badre et al. (2010); Miller and Cohen (2001). In fact, ample evidence  
167 indicates that cortical structures undergo Hebbian-like long term potentiation (LTP) and long term  
168 depression (LTD) Cooke and Bear (2010); Feldman (2009); Kirkwood, Rioult, and Bear (1996).  
169 However, despite the unsupervised nature of these processes, cortical representations are task-relevant  
170 and include appropriate sensorimotor mappings that lead to rewards Allen et al. (2017); Donahue and Lee  
171 (2015); Enel, Wallis, and Rich (2020); Jacobs and Moghaddam (2020); Petersen (2019); Tsutsui,  
172 Hosokawa, Yamada, and Iijima (2016). How could this arise from an unsupervised process? One  
173 possible explanation is that basal ganglia activate the appropriate cortical neurons during behaviors and  
174 the cortical network collectively consolidates high reward sensorimotor mappings via Hebbian-like  
175 learning Andalman and Fee (2009); Ashby, Ennis, and Spiering (2007); Hélie, Ell, and Ashby (2015);  
176 Tesileanu, Olveczky, and Balasubramanian (2017); Warren, Tumer, Charlesworth, and Brainard (2011).  
177 Previous computational accounts of this process have emphasized a consolidation function for the cortex  
178 in this process, which naively would beg the question of why duplicate a process that seems to function  
179 well in the basal ganglia and perhaps include a lot of details of the associated experience?

180 The answer to this question is the core of our proposal. We propose that the learning process is not a  
181 duplication, but instead that the reinforcement process in the basal ganglia selects thalamic control  
182 functions that subsequently activate cortical associations to allow flexible mappings across different  
183 contexts (Figure 2).

188 To understand this proposition, we need to take a closer look at the involvement of these distinct  
189 network elements in task learning. Learning in basal ganglia happens in corticostriatal synapses where  
190 the basic form of reinforcement learning is implemented. Specifically, the coactivation of sensory and  
191 motor cortical inputs generates eligibility traces in corticostriatal synapses that get captured by the  
192 presence or absence of DA Fee and Goldberg (2011); Fiete, Fee, and Seung (2007); Kornfeld et al.  
193 (2020). This RL algorithm is fast at acquiring simple associations but slow at generalization to other  
194 behaviors. On the other hand, the cortical plasticity operates in a much slower timescale but seems to  
195 allow flexible behaviors and fast generalization Kim, Johnson, Cilles, and Gold (2011); Mante, Sussillo,  
196 Shenoy, and Newsome (2013); Miller (2000); Miller and Cohen (2001). How does the cortex exhibit





184 **Figure 2. Two views of learning in the cortex** A. One possible view is that the Hebbian cortical plasticity consolidates the sensorimotor mapping from  
 185 BG to learn a stimulus-action mapping  $a_t = f(s_t)$ . B. We propose that thalamocortical systems perform meta-learning by consolidating the teaching signals  
 186 from BG to learn a context-dependent mapping  $a_t = f_c(s_t)$  where the context  $c$  is computed by past stimulus history and represented by different thalamic  
 187 activities.

197 slow synaptic plasticity and flexible behaviors at the same time? An explanatory framework is  
 198 **meta-learning** Botvinick et al. (2019); Wang et al. (2018), where the flexibility arises from network  
 199 dynamics and the generalization emerges from slow synaptic plasticity across different contexts. In other  
 200 words, synaptic plasticity stores a higher-order association between contexts and sensorimotor  
 201 associations while the network dynamics switches between different sensorimotor associations based on  
 202 this higher order association. However, properly arbitrating between synaptic plasticity and network  
 203 dynamics to store such higher order association is a nontrivial task Sohn, Meirhaeghe, Rajalingham, and  
 204 Jazayeri (2021). We propose that the thalamocortical system learns these dynamics, where the thalamus  
 205 provides control nodes that parametrize the cortical activity association space. Basal ganglia inputs to the  
 206 thalamus learn to select between these different control nodes directly implementing the interface  
 207 between weight adjustment and dynamical controls. Our proposal rests on the following three specific  
 208 points.

209 First, building on a line of the literature that shows diverse thalamocortical interaction in sensory,  
 210 cognitive and motor cortex, we propose that thalamic output may be described as control functions over  
 211 cortical computations. These control functions can be purely in the sensory domain like attentional

212 filtering, in the cognitive domain like manipulating working memory or in the motor domain like  
213 preparation for movement Bolkan et al. (2017); W. Guo, Clause, Barth-Maron, and Polley (2017);  
214 Z. V. Guo et al. (2017); Mukherjee et al. (2020); Rikhye, Gilra, and Halassa (2018); Saalman and  
215 Kastner (2015); Schmitt et al. (2017); Tanaka (2007); Wimmer et al. (2015); Zhou, Schafer, and  
216 Desimone (2016). These functions directly relate thalamic activity patterns to different cortical dynamical  
217 regimes and thus offer a way to establish higher order association between context and sensorimotor  
218 mapping within the thalamocortical pathways. Second, based on previous studies on direct and indirect  
219 BG pathways that influence most cortical regions Hunnicutt et al. (2016); Jiang and Kim (2018);  
220 Nakajima, Schmitt, and Halassa (2019); Peters, Fabre, Steinmetz, Harris, and Carandini (2021), we  
221 propose that BG hierarchically selects these thalamic control functions to influence activities of the cortex  
222 toward rewarding behavioral outcomes. Lastly, we propose that thalamocortical structure consolidate the  
223 selection of BG through a two timescales Hebbian learning process to enable meta-learning. Specifically,  
224 the faster corticothalamic plasticity learns the higher order association that enables flexible contextual  
225 switching with different thalamic patterns Marton, Seifkar, Luongo, Lee, and Sohal (2018); Rikhye et al.  
226 (2018) while the slower cortical plasticity learns the shared representations that allow generalization to  
227 new behaviors. Below, we will go over the supporting literature that leads us to this proposal.

## **MORE GENERAL ROLES OF THALAMOCORTICAL INTERACTION AND BASAL GANGLIA**

228 Classical literature has emphasized the role of the thalamus in transmitting sensory inputs to the cortex.  
229 This is because some of the better studied thalamic pathways are those connected to sensors on one end  
230 and primary cortical areas on another Hubel and Wiesel (1961); Lien and Scanziani (2018); Reinagel,  
231 Godwin, Sherman, and Koch (1999); Sherman and Spear (1982); Usrey, Alonso, and Reid (2000). From  
232 that perspective, thalamic neurons being devoid of lateral connection transmit their inputs (e.g. from the  
233 retina in the case of the lateral geniculate nucleus (LGN)) to the primary sensory cortex (V1 in this same  
234 example case) and the input transformation (center-surround to oriented edges) occurs within the  
235 cortex Hoffmann, Stone, and Sherman (1972); Hubel and Wiesel (1962); Lien and Scanziani (2018);  
236 Usrey et al. (2000). In many cases, these formulations of thalamic “relay” have generalized to how motor  
237 and cognitive thalamocortical interactions may be operating. However, in contrast to the classical relay

view of the thalamus, more recent studies have shown diverse thalamic functions in sensory, cognitive and motor processing Bolkan et al. (2017); W. Guo et al. (2017); Z. V. Guo et al. (2017); Rikhye et al. (2018); Saalman and Kastner (2015); Schmitt et al. (2017); Tanaka (2007); Wimmer et al. (2015); Zhou et al. (2016). For example in mice, sensory thalamocortical transmission can be adjusted based on PFC-dependent, top-down biasing signals transmitted through non-classical basal ganglia pathways involving the thalamic reticular nucleus (TRN) Nakajima et al. (2019); Phillips, Kambi, and Saalman (2016); Wimmer et al. (2015). Interestingly, these task-relevant PFC signals themselves require long range interactions with the associative mediodorsal (MD) thalamus to be initiated, maintained and flexibly switched Rikhye et al. (2018); Schmitt et al. (2017); Wimmer et al. (2015). One can also observe nontrivial control functions in the motor thalamus. Motor preparatory activities in the anterior motor cortex (ALM) show persistent activities that predicted future actions. Interestingly, the motor thalamus also shows similar preparatory activities that predict future actions and by optogenetically manipulate the motor thalamus activities, the persistent activities in ALM quickly diminished Z. V. Guo et al. (2017). Recently, Mukherjee, Lam, Wimmer, and Halassa (2021) discovers two cell types within MD thalamus differentially modulates the cortical evidence accumulation dynamics depending on if the evidences are conflicting or sparse to boost signal-to-noise ratio in decision making. Based on the above studies, we propose that the thalamus provides a set of control functions to the cortex. Specifically, cortical computations may be flexibly switched to different dynamical modes by activating a particular thalamic output that corresponds to that mode.

On the other hand, the selective role of BG in motor and cognitive control also has dominated the literature because thalamocortical-basal ganglia interaction is the most well studied in frontal systems Cox and Witten (2019); Makino et al. (2016); McNab and Klingberg (2008); Monchi, Petrides, Strafella, Worsley, and Doyon (2006); Seo et al. (2012). However, classical and contemporary studies have recognized that all cortical areas, including primary sensory areas project to the striatum Hunnicutt et al. (2016); Jiang and Kim (2018); Peters et al. (2021). Similarly, the basal ganglia can project to the more sensory parts of the thalamus through lesser-studied pathways to influence the sensory cortex Hunnicutt et al. (2016); Nakajima et al. (2019); Peters et al. (2021). Specifically, a non-classical BG pathway projects to TRN which in turn modulates the activities of LGN to influence sensory thalamocortical transmission Nakajima et al. (2019). On the other hand, it has also been argued that BG

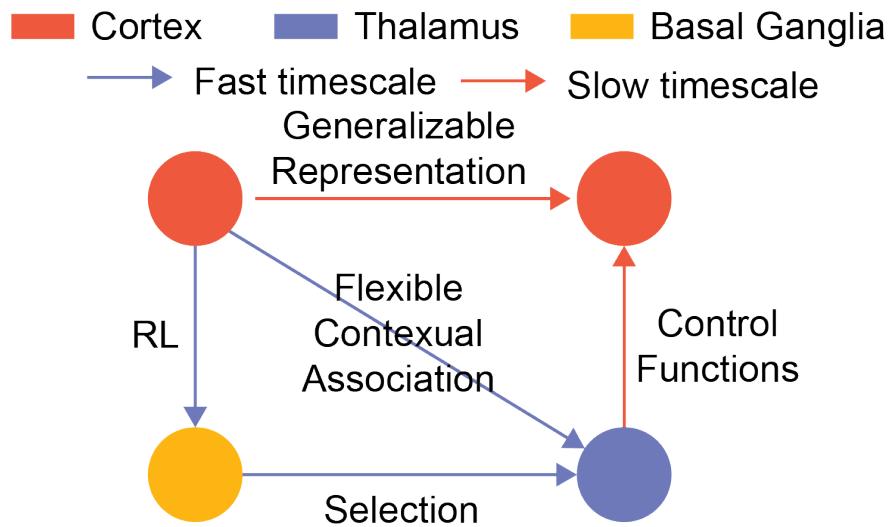
267 are involved in gating working memory McNab and Klingberg (2008); Voytek and Knight (2010). This  
268 shows that BG has a much more general role than classical action and action strategy selection.  
269 Therefore, combining with our proposals on thalamic control functions, we propose that BG  
270 hierarchically selects different thalamic control functions to influence all cortical areas in different  
271 contexts through reinforcement learning.

272 Furthermore, there are series of the work that indicates the role of BG to guide plasticity in  
273 thalamocortical structures Andalman and Fee (2009); Fiete et al. (2007); Héli e et al. (2015); Mehaffey  
274 and Doupe (2015); Tesileanu et al. (2017). In particular, there is evidence that BG is critical for the initial  
275 learning and less involved in the automatic behaviors once the behaviors are learned across different  
276 species. In zebra finches, the lesion of BG in adult zebra finch has little effects on song production, but  
277 the lesion of BG in juvenile zebra finch prevents the bird from learning the song Fee and Goldberg  
278 (2011); Scharff and Nottebohm (1991); Sohrabji, Nordeen, and Nordeen (1990). Similar patterns can be  
279 observed in people with Parkinson’s disease. Parkinson’s patients who have a reduction of DA and  
280 striatal defects have troubles in solving procedural learning tasks but can produce automatic behaviors  
281 normally Asmus, Huber, Gasser, and Sch ols (2008); Soliveri, Brown, Jahanshahi, Caraceni, and Marsden  
282 (1997); Thomas-Ollivier et al. (1999). This behavioral evidence suggests that thalamocortical structures  
283 consolidate the learning from BG as the behaviors become more automatic. Furthermore, on the synaptic  
284 level, a songbird learning circuit also demonstrates this cortical consolidation motif Mehaffey and Doupe  
285 (2015); Tesileanu et al. (2017). In a zebra finch, the premotor nucleus HVC (a proper name) projects to  
286 the motor nucleus robust nucleus of the arcopallium (RA) to produce the song. On the other hand, RA  
287 also receives BG nucleus Area X mediated inputs from the lateral nucleus of the medial nidopallium  
288 (LMAN). The latter pathway is believed to be a locus of reinforcement learning in the songbird circuit.  
289 By burst stimulating both input pathways in different time lags, one can discover that HVC-RA and  
290 LMAN-RA underwent opposite plasticity Mehaffey and Doupe (2015). This suggests that the learning is  
291 gradually transferred from LMAN-RA to HVC-RA pathway Fee and Goldberg (2011); Mehaffey and  
292 Doupe (2015); Tesileanu et al. (2017). This indicates a general role of BG as the trainer for cortical  
293 plasticity.

## **THE THALAMOCORTICAL STRUCTURE CONSOLIDATES THE BG SELECTIONS ON THALAMIC CONTROL FUNCTIONS IN DIFFERENT TIMESCALES TO ENABLE META-LEARNING.**

294 In this section, in addition to BG's role as the trainer for cortical plasticity, we further propose that BG is  
295 the trainer in two different timescales for thalamocortical structures to enable meta-learning. The faster  
296 timescale trainer trains the corticothalamic connections to select the appropriate thalamic control  
297 functions in different contexts while the slower timescale trainer trains the cortical connections to form a  
298 task-relevant and generalizable representation.

299 From the songbird example, we see how thalamocortical structures can consolidate simple associations  
300 learned through the basal ganglia. To enable meta-learning, we propose that this general network  
301 consolidation motif operates over two different timescales within thalamocortical-basal ganglia  
302 interactions (Figure 3). First, combining the idea of thalamic outputs as control functions over cortical  
303 network activity patterns and the basal ganglia selecting such functions, we frame learning in basal  
304 ganglia as a process that connects contextual associations (higher order) with the appropriate dynamical  
305 control that maximizes reward at the sensorimotor level (lower order). Under this framing,  
306 corticothalamic plasticity consolidates the higher order association within a fast timescale. This allows  
307 flexible switching between different thalamic control functions in different contexts. On the other hand,  
308 the cortical plasticity consolidates the sensorimotor association over a slow timescale to allow shared  
309 representation that can generalize across different contexts. As the thalamocortical structures learn the  
310 higher order association, the behaviors become less BG-dependent and the network is able to switch  
311 between different thalamic control functions to induce different sensorimotor mappings in different  
312 contexts. By having two learning timescales, animals can conceivably both adapt quickly in changing  
313 environments with fast learning of corticothalamic connections while maintaining the important  
314 information across the environment in the cortical connections. One should note that this separation of  
315 timescales is independent from different timescales across cortex Gao, van den Brink, Pfeffer, and Voytek  
316 (2020); J. D. Murray et al. (2014). While different timescales across cortex allows animals to process  
317 information differentially, the separation of corticothalamic and cortical plasticity allows the  
318 thalamocortical system to learn the higher contextual association to modulate cortical dynamics flexibly.



319 **Figure 3. Two timescales learning in thalamocortical structures** We propose that one can learn the thalamocortical structure to enable meta-learning by  
 320 applying the general network motif in two different timescales. First, one can learn the corticothalamic connections by applying the motif with  
 321 a faster timescale. This allows the network to consolidate flexible switching behaviors. Second, one can learn the cortical connections by applying the motif  
 322 on the orange loop in a slower timescale. This allows cortical neurons to develop a task-relevant shared representation that can generalize across contexts.

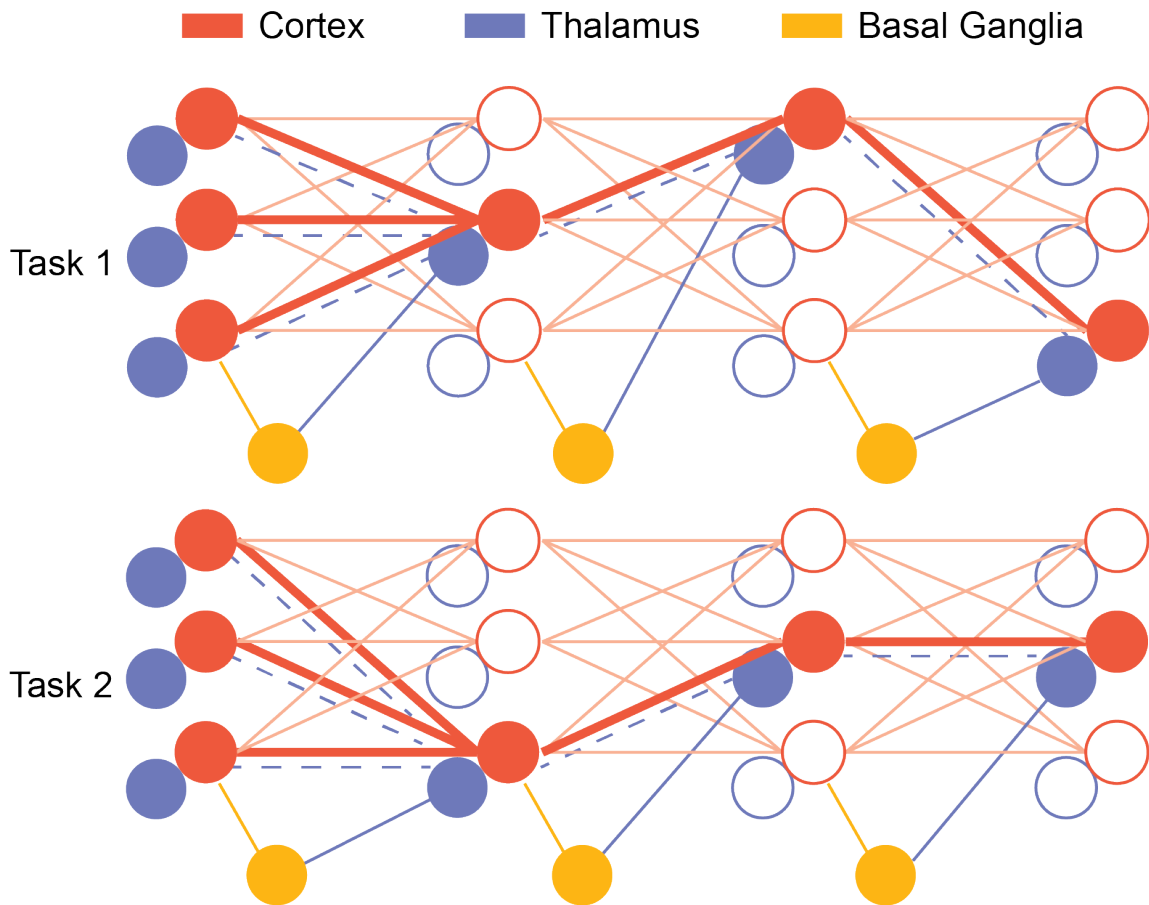
323 Some anatomical observations support this idea. The thalamostriatal neurons has a more modulatory  
 324 role to the cortical dynamics in a diffusive projection while thalamocortical neurons has a more driver  
 325 role to the cortical dynamic in a topographically restricted dense projection Sherman and Guillery (2005).  
 326 This indicates that thalamostriatal neurons might serve as the role of control functions in the faster  
 327 consolidation loop with the feedback to striatum to conduct credit assignment. On the other hand,  
 328 thalamocortical neurons might be more involved in the slower consolidation loop with the feedback to  
 329 striatum coming from the cortex to train the common cortical representation across contexts.

330 In summary, this two timescales network consolidation scheme provides a general way for BG to guide  
 331 plasticity in the thalamocortical architecture to enable meta-learning and thus solves structural credit  
 332 assignment as a special case. Along these lines, experimental evidence supports the notion that when  
 333 faced with multi-sensory inputs, the BG can selectively disinhibit a modality-specific subnetwork of the  
 334 thalamic reticular nucleus (TRN) to filter out the sensory inputs that are not relevant to the behavior  
 335 outcomes and thus solve the structural credit assignment problem.

336 In the discussion above, we discuss our proposal under a general formulation of thalamic control  
337 functions. In the next section, we will specify other thalamic control functions suggested by recent  
338 studies and observe how they can solve continual learning under this framework as well.

## **THE THALAMUS SELECTIVELY AMPLIFIES FUNCTIONAL CORTICAL CONNECTIVITY AS A SOLUTION TO CONTINUAL LEARNING AND CATASTROPHIC FORGETTING.**

339 One of the pitfalls of the artificial neural network is catastrophic forgetting. If one trains an artificial  
340 neural network on a sequence of tasks, the performance on the older task will quickly deteriorate as the  
341 network learns the new task French (1999); Kemker et al. (2018); Kumaran et al. (2016); McCloskey and  
342 Cohen (1989); Parisi et al. (2019). On the other hand, the brain can achieve *continual learning*, the ability  
343 to learn different tasks in different contexts without catastrophic forgetting and even generalize the  
344 performance to novel context Lewkowicz (2014); M. M. Murray et al. (2016); Power and Schlaggar  
345 (2017); Zenke, Gerstner, and Ganguli (2017). There are three main approaches in machine learning in  
346 dealing with catastrophic forgetting. First, one can use the regularization method to mostly update the  
347 weights that are less important to the prior tasks Fernando et al. (2017); Jung, Ju, Jung, and Kim (2018);  
348 Kirkpatrick et al. (2017); Li and Hoiem (2018); Maltoni and Lomonaco (2019); Zenke, Poole, and  
349 Ganguli (2017). This idea is inspired by experimental and theoretical studies on how synaptic information  
350 is selectively protected in the brain Benna and Fusi (2016); Cichon and Gan (2015); Fusi, Drew, and  
351 Abbott (2005); Hayashi-Takagi et al. (2015); Yang, Pan, and Gan (2009). However, it is unclear how to  
352 biologically compute the importance of each synapse to prior tasks nor how to do global regularization  
353 locally. Second, one can also use a dynamic architecture in which the network expands the architecture  
354 by allocating a subnetwork to train with the new information while preserving old information Cortes,  
355 Gonzalvo, Kuznetsov, Mohri, and Yang (2017); Draelos et al. (2017); Rusu et al. (2016); Xiao, Zhang,  
356 Yang, Peng, and Zhang (2014). However, this type of method is not scalable since the number of neurons  
357 needs to scale linearly with the number of the task. Lastly, one can use a memory buffer to replay past  
358 tasks to avoid catastrophic forgetting by interleaving the experience of the past tasks with the experience  
359 of the present task Kemker and Kanan (2018); Kumaran et al. (2016); McClelland et al. (1995); Shin,  
360 Lee, Kim, and Kim (2017). However, this type of method cannot be the sole solution as the memory  
361 buffer needs to scale linearly with the number of the tasks and potentially the number of the trials.



362 **Figure 4. A thalamocortical architecture with interaction with BG for continual learning** During task execution, BG selects thalamic neurons that  
 363 amplify the relevant cortical subnetwork. This protects other parts of the network that are important for another context from being overwritten. When the  
 364 other task comes, BG selects other thalamic neurons and since the synapses are protected from the last task, animals can freely switch from different tasks  
 365 without forgetting the previous tasks. Furthermore, as the corticothalamic synapses learn how to select the right thalamic neurons in a different context (blue  
 366 dash line), task execution can become less BG dependent.

367 We propose that the thalamus provides another way to solve continual learning and catastrophic  
 368 forgetting via selectively amplifying parts of the cortical connections in different contexts (Figure 4).  
 369 Specifically, we propose that a population of thalamic neurons topographically amplify the connectivity  
 370 of cortical subnetworks as their control functions. During a behavioral task, BG selects subsets of the  
 371 thalamus which selectively amplify the connectivity of cortical subnetworks. Because of the  
 372 reinforcement learning in BG, the subnetwork that is the most relevant to the current task will be more  
 373 preferentially activated and updated. By selecting only the relevant subnetwork to activate in one context,



374 the thalamus protects other subnetworks which can have useful information in another context from being  
375 overwritten. The corticothalamic structures can then consolidate these BG-guided flexible switching  
376 behaviors via our proposed network motif and the switching becomes less BG-dependent. Furthermore,  
377 our proposed solution has implications on generalization as well. Different tasks can have principles in  
378 common that can be transferred. For example, although the rules of chess and Go are very different,  
379 players in both games all need to predict what the other players are going to do and counterattack based  
380 on the prediction. Since BG selects the subnetwork at each hierarchy that is most relevant to the current  
381 tasks, in addition to selecting different subnetworks to prevent catastrophic forgetting, BG can also select  
382 subnetworks that are beneficial to both tasks as well to achieve generalization. Therefore, the cortex can  
383 develop a modular hierarchical representation of the world that can be easily generalized.

384 The idea of protecting relevant information from the past tasks to be overwritten has been applied  
385 before computationally and has decent success in combating catastrophic forgetting in deep learning  
386 [Kirkpatrick et al. \(2017\)](#). Experimentally, we also have found thalamic neurons selectively amplify the  
387 cortical connectivity to solve the continual learning problem. In a task where the mice need to switch  
388 between different sets of task cues that guided the attention to the visual or auditory target, the  
389 performance of the mice does not deteriorate much after switching to the original context which is an  
390 indication of continual learning [Rikhye et al. \(2018\)](#). Electrophysiological recording of PFC and  
391 mediodorsal thalamic nucleus (MD) neurons, we discovered that PFC neurons preferentially code for the  
392 rule of the attention while MD neurons preferentially code for the contexts of different sets of the cues.  
393 Thalamic neurons that encode the task-relevant context translate this neural representation into the  
394 amplification of cortical activity patterns associated with that context (despite the fact that cortical  
395 neurons themselves only encode the context implicitly). These experimental observations are consistent  
396 with our proposed solution: by incorporating the thalamic population that can selectively amplify  
397 connectivity of cortical subnetworks, the thalamus and its interaction with cortex and BG solve the  
398 continual learning problem and prevent catastrophic forgetting.

## CONCLUSION

399 In summary, in contrast to the traditional relay view of the thalamus, we propose that thalamocortical  
400 interaction is the locus of meta-learning where the thalamus provides cortical control functions, such as

401 sensory filtering, working memory gating or motor preparation, that parametrize the cortical activity  
402 association space. Furthermore, we propose a two timescale learning consolidation framework where BG  
403 hierarchically selects these thalamic control functions to enable meta-learning, solving the credit  
404 assignment problem. The faster plasticity learns contextual associations to enable rapid behavioral  
405 flexibility while the slower plasticity establishes cortical representation that generalizes. By considering  
406 the recent observation of the thalamus selectively amplifying functional cortical connectivity, the  
407 thalamocortical-basal ganglia network is able to flexibly learn context-dependent association without  
408 catastrophic forgetting while generalizing to the new contexts. This modular account of the  
409 thalamocortical interaction may seem to be in contrast with the recent proposed dynamical perspectives  
410 Barack and Krakauer (2021) on thalamocortical interaction in which the thalamus shapes and constrains  
411 the cortical attractor landscapes Shine (2021). We would like to argue that both the modular and  
412 dynamical perspectives are compatible with our proposal. The crux of the perspectives is that the  
413 thalamus provides control functions that parametrize cortical dynamics and these control functions can be  
414 of modular nature or of dynamical nature depending on their specific input-output connectivity. Flexible  
415 behaviors can be induced either by selecting the control functions that amplify the appropriate cortical  
416 subnetworks or those that adjust the cortical dynamics to the appropriate regimes.

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