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CHAPTER

# 34. Models of Thalamocortical Interactions in Motor Control 🔓

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## Abstract

The ever-increasing accumulation of experimental results from the thalamocortical system has driven improvements in theories and models of circuit mechanisms in motor control. In this chapter, the authors give a historical overview of the development of such theories, and propose a taxonomy for categorizing models into types according to 2 principal features: (1) whether they assume a representational or dynamical function for motor cortex, and (2) whether thalamus acts as a feedforward input to, or a bidirectional loop with, cortex. They show that technical advances in experimental and theoretical approaches have led to a conceptualization of the thalamocortical circuit as a mechanism for efficiently reconfiguring cortical dynamics. In this framework, context-specific thalamocortical loops can refine cortical computations to solve multiple tasks accurately and robustly. The chapter demonstrates that throughout the history of modeling in the thalamocortical circuit, mathematical insights have illuminated new theories and proposed new experiments.

**Keywords:** thalamocortical, corticothalamic, computational modeling, motor control, cortical circuits
**Subject:** Neuroscience
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# Introduction

Understanding motor control is a fundamental goal of systems neuroscience. Yet a major question remains regarding the role of the interactions between the thalamus and cortex in motor computations. There have been multiple recent models proposed to interrogate this. Thus, it is now timely to review the state of these modeling efforts. Importantly, these recent models of thalamocortical interactions have benefited from the significant expansion of experimental data—in terms of behavior, anatomy, and physiology—and have positioned the role of understanding this circuit centrally in terms of our overall conception of motor control.

We begin by placing models of thalamocortical interactions within the context of motor system modeling writ large, which has greatly expanded our understanding of motor function and control. This body of work has operated at multiple levels of abstraction, from detailed biophysical models of individual neurons (for which there is a vast literature, including in the thalamus; see **Section II** of this volume) to computational and algorithmic models that do not speak directly to implementations within the brain (e.g.,

Todorov and Jordan, 2002). A class of models that has particular appeal considers the firing rates of individual neurons or populations of neurons, and the correlations between these firing rates across neurons and populations (Gerstner et al., 2014). These network models permit the interrogation of interactions between brain areas and their impacts on behavior. They are thus of particular relevance for the study of thalamocortical interactions and form the focus of our discussion in this chapter.

Firing-rate models themselves can be further subdivided into those that describe neural computation in terms of mean firing rates that are static over some relevant time period and those that consider the moment-by-moment firing-rate dynamics. The former view is inherited from the seminal work of Hubel and Wiesel in visual neuroscience that ascribes to individual cortical cells "receptive fields": static spatiotemporal representations that extract cell-specific statistics from external stimuli and that emerge through several steps of feedforward processing from thalamus to higher-order cortical areas (Hubel and Wiesel, 1962; Yamins et al., 2014). Similarly, motor system models that attribute to individual motor cortical neurons the representation of specific features of movements and that ignore time have been applied to understand neural computation in the motor system (Georgopoulos et al., 1982). However, recent efforts for modeling motor control have followed the alternative perspective in which motor cortical activity results from ongoing continuous dynamics (Shenoy et al., 2013). In this conceptualization, the cortical population as a whole represents instantaneous muscle commands.

As we shall see in detail, despite the fact that the motor cortex and premotor cortex are innervated by multiple motor thalamic nuclei such as the ventromedial (VM), ventroanterior (VA), and ventrolateral (VL) nucleus (see **Chapters 31, 33**, **and 35 in Section VI**), both static and dynamic models of motor cortical function have often either ignored motor thalamus entirely or have relegated the thalamus to serving as a relay in the flow of information to motor cortex (Doya, 2000). However, a growing body of research explicitly parses the role of thalamocortical interactions and proposes specific computations that this circuit motif enables (Kao et al., 2021; Logiaco et al., 2021; Shine, 2021; Recanatesi et al., 2022). This work considers the importance of corticothalamic feedback in facilitating motor execution and learning (see **Section IV** of this volume).

We propose a taxonomy of models of thalamocortical interactions in the motor system that will permit productive comparison. This taxonomy evaluates models along two dimensions: (1) whether static versus dynamic interpretations of cortical representations are important; and (2) how the anatomy of the circuit—that is, both the ↳ feedforward and feedback connections between thalamus and cortex—informs motor function. In view of the recent evidence suggesting that motor cortical dynamics drive motor output in real time for at least some mammalian behaviors (Shenoy et al., 2013; Sauerbrei et al., 2019; Guo et al., 2021), important insights can be gained through the recent theoretical and modeling advances that dissect the contribution of the recurrent cortical and thalamocortical connectivity in shaping rich multi-area dynamics.

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## Historical Overview and Taxonomy of Motor Thalamocortical Models

We begin by offering an overview of the history of models of motor control and how they have influenced the development of models of thalamocortical interactions, including the possible influence that earlier results and approaches of sensory neuroscience have had on the field of motor control. This will lead us to define three important classes of models of thalamocortical interactions. In later sections, we dive into the mechanistic details of these classes of models.

## Positioning the Thalamus within Evolving Models of Cortical Motor Control

One of the earliest lines of research for modeling motor cortical function (Georgopoulos et al., 1982) views motor cortical activity as a distributed representation of relatively static parameters of movements, such as reach angles for arm reaches. As these variables are abstract and slower than the movement timescales, the underlying assumption is that their influence on motor control would be mediated by modulation of a downstream dynamic circuit. This view was influenced by the foundational work of Hubel and Wiesel (1962) in the visual cortex. Similar to the methods used to map receptive fields in sensory areas, this framework involves computing a "tuning curve" that describes the neuron's mean firing rate when an animal performs different behaviors to find the specific movement feature that it "encodes." Anatomically, the thalamus is positioned as a relatively low-dimensional upstream input (see **Sections IV and V** of this volume) with no internal excitatory recurrence (see **Section II**). Thus, in these models, the role of thalamus is a preliminary feedforward processing step, for example, a simple relay (Chevalier and Deniau, 1990). In this scenario—which encompasses an ensemble of models we shall refer to as "Type I"—the thalamus either plays a minor feedforward processing role or is even not explicitly differentiated in the model.

However, two lines of evidence suggest that motor cortical activity should not be viewed as a collection of tuning curves, but rather as a dynamical system whose instantaneous population activity is read out by downstream circuits for online motor control. First, with respect to anatomy, the primary motor cortex is a large recurrent neural network that has embedded corticospinal tract neurons that project to the motor periphery (Friedli et al., 2015). Second, with respect to function, electrophysiology experiments have measured strong correlations between instantaneous activity in the motor cortex and moment-by-moment muscle activity (Shenoy et al., 2013). Given this, some models—which we shall call "Type II"—account for the thalamus as an input to a dynamical cortical system that drives movement.

Finally, additional anatomical data (see **Section IV** of this volume) has established that the thalamocortical circuit is bi-directional, with both feedforward connections from the thalamus and feedback connections from the cortex. Thus, a few recently developed models have considered the loop between the cortex and thalamus (Kao et al., 2021; Logiaco et al., 2021; Lakshminarasimhan et al., 2022; Recanatesi et al., 2022) as essential to shape circuit dynamics to drive downstream movements. We shall call such models "Type III."

It is important to point out that these model classes arise from specific choices made by modelers in order to concentrate on features of the neurobiology that are assumed to be most important. Thus, though Type I and Type II models are simpler, the decision to omit certain details was made to serve the goal of illustrating specific computational hypotheses in a parsimonious manner.

## A Proposed Taxonomy of Motor Thalamocortical Models and Its Limitations

Given the historical development of motor thalamocortical models reviewed above, we propose a taxonomy of these according to two axes: (1) whether they assume that motor cortex represents quasi-static high-level parameters of movements or implements complex dynamics that more directly drive muscles; and (2) whether the thalamus acts as a source of external input to the cortex or as a cortico-thalamo-cortical loop that intrinsically participates in the circuit's dynamics (Figure 34.1).
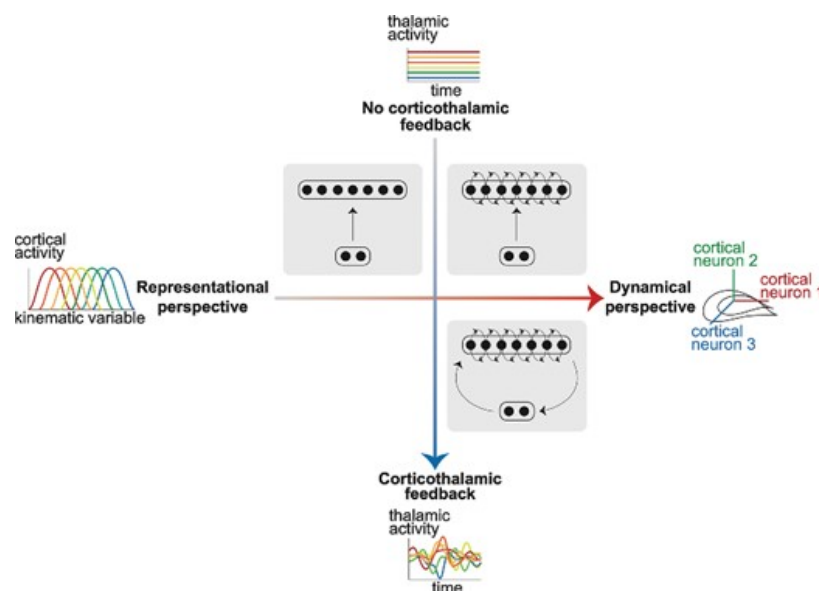
**Figure 34.1.** A proposed taxonomy of motor thalamocortical models. The horizontal axis delineates models according to the function they attribute to the motor cortex (representational vs. dynamical). The vertical axis identifies models according to the connectivity between the cortex and the thalamus (feedforward vs. loopy).

Importantly, it should be noted that these two taxonomic features help conceptualize differences between models that are often of a graded rather than categorical nature. For example, with respect to the static versus dynamic axis, it is possible to design a dynamical model such that a static movement kinematic parameter can be decoded from the population activity at all times (Bachschmid-Romano et al., 2022). In this case, the ↳ network dynamics do not contribute to motor control, but rather are included to improve biological realism given the established nature of the motor cortex as a recurrent system and the non-stationarity of motor neural activity seen in recordings. In addition, with respect to the feedforward versus loop axis, the computational consequences of this dichotomy will depend on specific modeling assumptions. For example, the complexity of the nonlinearities in the cortical network can dictate how the cortical dynamics can be modulated, such that even an external input can have a nontrivial impact.

Another important caveat is that different motor thalamocortical subcircuits may fall in different regions along these proposed axes. For instance, it has been suggested that basal ganglia–recipient thalamus may be connected to the motor cortex in a more bidirectional fashion than cerebellum-recipient thalamus (Bosch-Bouju et al., 2013). In addition, while we chose to organize thalamocortical models along these axes, there are other model characteristics worth considering, such as the origin and nature of the extra-cortical signals received by the modeled thalamus (see **Chapter 31 in Section VI**) and the position of the modeled circuit within the premotor to motor hierarchy (see Section VIII). However, despite these considerations, we will argue below that the axes depicted in Figure 34.1 can be helpful guidelines to orient the reader when navigating the space of thalamocortical models of motor function.

## Type I Models: Thalamus as a Relay of Kinematic Variables

As stated in the previous section, early attempts to investigate motor control were heavily influenced by our understanding of sensory processing and, in particular, visual perception. As a result, models of thalamocortical interactions were initially grounded in a perspective in which the motor cortex exerted control over movements by encoding kinematic variables such as the location and/or direction of movements. In this section, we review experimental evidence in favor of representational theories of motor control and the computational role ascribed to thalamocortical interactions by such theories.

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## Background and Motivation

Inspired by seminal studies of the visual system which identified neurons tuned to static latent variables such as spatial orientation (Hubel and Wiesel, 1962) and the direction of visual motion (Albright, 1984), neural activity in the motor cortex was interpreted in relation to movement parameters such as the joint angle (Evarts, 1968), speed (Inoue et al., 2018), and the direction of movement

(Georgopoulos et al., 1982). For example, neural responses in the primary motor cortex (M1) of monkeys performing ↳ ballistic reaching movements were shown to depend on the endpoint of the movement. Then, the change (relative to baseline) in the average firing rate of individual cortical neurons $h$ could be captured by a cosine tuning function of the movement direction $\theta$ (i.e., $h \propto cos(\theta - \theta_0)$ where $\theta_0$ denotes the preferred movement direction (Figure 34.2A). The preferred direction of neurons has been shown to vary systematically, constituting a topographic map (Georgopoulos et al., 2007). Therefore, an observer of the neural population in M1 can reliably decode the direction of the monkey's arm movements with high precision (Georgopoulos et al., 1982, 2007). How is this representation of kinematic variables established?
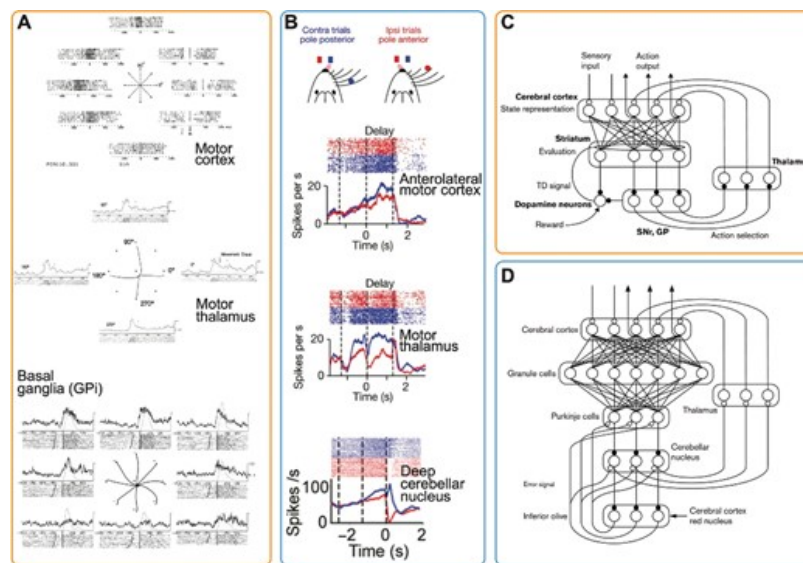


**Figure 34.2.** Type I models. (A). Responses of example neurons from the primate primary motor cortex (top: from Georgopoulos et al., 1982), motor thalamus (middle: from Inase et al., 1996), and the internal segment of the Globus pallidus (GPi, bottom: from Turner and Anderson, 1997) showing tuning to the direction of arm movement. (B). Activity of neurons in the mouse ALM (top: from Guo et al., 2017), motor thalamus (middle: from (Guo et al., 2017), and deep cerebellar nucleus (bottom: from Gao et al., 2018) showing tuning to the *upcoming* lick direction (delay period activity). (C–D). Standard models of the cortico-basal ganglia-thalamocortical loop (C) and the cortico-cerebello-thalamocortical loop (D) assume that motor thalamus is a relay of subcortical signals to the cortex (from Doya, 2000). Data and the model panels are color coded (orange: basal-ganglia-thalamo-cortical; blue: cerebello-thalamo-cortical).

In primary visual cortex, feature tuning is largely a consequence of the precise wiring of feedforward inputs from the retina through the lateral geniculate nucleus of the thalamus, constituting a labeled line code (Hubel and Wiesel, 1962; Chapman and Stryker, 1992; Clay Reid and Alonso, 1995). In contrast, the premotor and motor cortices are innervated by multiple motor thalamic nuclei such as the ventromedial (VM), ventroanterior (VA), and ventrolateral (VL) nucleus, which in turn receive inputs from different regions such as the basal ganglia and the cerebellum. Studies have found no clear evidence for a direction signal in the cerebellum (Trouche and Beaubaton, 1980; Thach et al., 1992; Horne and Butler, 1995). In contrast, the output nuclei of the basal ganglia (GPi/SNr) encode movement direction (Georgopoulos et al., 1983; Turner and Anderson, 1997), as do some neurons in the motor thalamus (Butler et al., 1996). Furthermore, several studies have shown that the activity of neurons in the motor thalamus is triggered by the presentation of a cue and peaks prior to movement onset (Figure 34.2A; Strick, 1976; Butler et al., 1992; Forlano et al., 1993). Lesion studies

have also consistently implicated the basal ganglia–thalamocortical pathway in movement initiation (Groenewegen, 2003). Against ↳ the backdrop of the models developed to account for the computational role of basal ganglia in movement, a verbal theory

without a precise mathematical underpinning has emerged which treats the motor thalamus as a relay of the basal ganglia output to the motor cortex.

Recent studies in mice have used licking behavior to study the role of another prominent pathway through the motor thalamus—the cerebello-thalamocortical pathway—in motor preparation. Similar to the representation of arm movement direction in the motor cortex of monkeys, rodent studies have found a robust representation of the licking direction in the mouse premotor cortex (anterolateral motor cortex, or ALM, to be specific), except these representations were activated *before* movement (Figure 34.2B; Guo et al., 2017). Subsequent work has shown that similar representations are found in the deep cerebellar nuclei (DCN), the output nuclei of the cerebellum (Figure 34.2B). Inactivating the DCN or the VM nucleus of the thalamus (which receives inputs from the DCN) abolishes preparatory activity in the cortex (Gao et al., 2018; Chabrol et al., 2019). Analogous to the role of basal ganglia–recipient motor thalamus, these studies have led to a view of the cerebellum-recipient motor thalamus as a relay of preparatory signals from the cerebellum to the premotor cortex.

## Model Details

In this section, we review specific examples of Type I models, focusing on basal ganglia and cerebellar-recipient thalamic nuclei. However, motor thalamus also receives inputs from other subcortical structures, such as the superior colliculus and the midbrain (see **Chapter 31 in Section VI**) which could also be modeled along similar lines.

### Basal Ganglia–Recipient Thalamic Neurons

Models proposing motor thalamus as a relay of basal ganglia commands to the cortex have been in place since the early 1990s (Albin et al., 1989; Chevalier and Deniau, 1990). Let $s$ and $r$ denote the activity levels in the basal ganglia output nuclei (GPi/SNr) and motor thalamus, respectively. Since neurons in GPi/SNr exhibit high spontaneous firing rates (s >> 0) and release GABA into the motor thalamus (Chevalier and Deniau, 1990), these models assume that motor thalamic neurons are chronically inhibited; that is, $r = f(\delta - s) \approx 0$ where $f$ is a rectifying nonlinearity with a small threshold $\delta$. However, when the basal ganglia is activated, the activity of a subset of neurons in GPi/SNr is suppressed ($s < \delta$) and their downstream thalamic targets are transiently disinhibited. In this manner, the thalamus is able to relay commands from the basal ganglia, selectively activating specific representations in the motor cortex (Figure 34.2C; Doya, 2000). The specific mechanism of thalamic disinhibition has since been refined to incorporate a role for the hyperdirect pathway in the basal ganglia. Briefly, the updated view suggests that a delicate interplay between the synaptic latencies and the polarities of parallel cortico-basal ganglia pathways—hyperdirect, direct, and indirect—triggers a sequence of events that lead to inhibition, followed by disinhibition, and then back to inhibition of a subset of neurons in the motor thalamus, resulting in the transient thalamic activation that typically precedes movement initiation (Nambu et al., 2002; Polyakova et al., 2020).

### Cerebellar-Recipient Thalamic Neurons

Unlike basal ganglia–recipient thalamic neurons, the cerebellar-recipient thalamus is not under chronic inhibition from the cerebellum. Therefore, the cerebellar outputs (DCN) influence the motor thalamus primarily by excitation rather than disinhibition: that is, $r = f(s - \delta)$. That said, similar to the basal ganglia–thalamocortical pathway above, thalamic neurons targeted by the cerebellothalamic tracts could function as a relay (Figure 34.2D; Doya, 2000). Consistent with this, inhibiting the preparatory activity in the DCN abolishes preparatory activity in the premotor cortex (Gao et al., 2018), which suggests that the motor thalamus allows the cerebellum to mediate transitions between cortical states (Li and Mrsic-Flogel, 2020). An important caveat in interpreting these data is that DCN inactivation induces a mixture of excitation and inhibition in the thalamus and cortex, suggesting that VM thalamus might be more than just a relay.

## Thalamocortical Interactions

In the models that consider motor thalamus as a relay, thalamic influence on the cortex can be described as a feedforward drive: $h = f(Ur)$, where $h$ denotes cortical activity, $U$ denotes the thalamocortical connectivity matrix, and $f$ is the nonlinearity of the cortical neurons. An interesting implication of these types of feedforward relay models is that the structure of the thalamocortical weights should dictate the degree to which cortical neurons are tuned. Random thalamocortical interactions would produce a distributed population code resulting in mixed selectivity of preparatory or movement-related parameters in individual cortical neurons. Alternatively, thalamocortical connectivity might be structured by developmental programs or by plasticity-based mechanisms within the cortex (Biane et al., 2016) to ensure high representational fidelity at the level of single neurons. Therefore, a systematic comparison of subcortical and cortical selectivity in single neurons can shed light on the structure of thalamocortical interactions.

## Limitations

A limitation of the representational view assumed by the above models is that they cannot capture how the temporal heterogeneity exhibited by cortical neurons is correlated with moment-by-moment muscle activity and movement kinematics (Shenoy et al., 2013). The significance of considering temporal dynamics in the context of motor control becomes clear when contrasting the nature of computations performed by perceptual and motor systems. In perception, the input to the system is generated externally (i.e., in the world) and the role of the perceptual system is to invert that generative model to infer the latent states responsible for those inputs. In contrast, the goal of motor control is to generate appropriate muscle commands to achieve a desired change of state. Therefore, a purely representational account cannot constitute a causal theory of movement production. A recognition of this limitation has led to the development of models based on dynamical systems theory, which are described below.

# Type II Models: Thalamus as an Afferent to Dynamical Cortical Models

Motivated to more accurately capture the anatomy and activity features of cortex (Shenoy et al., 2013; Rikhye et al., 2018) or by functional considerations positioning the cortical output as a direct driver of downstream motor effectors (Friedli et al., 2015), several models have moved away from viewing thalamocortical networks as computing static representations and turned instead to considering a dynamical system framework. A subset of these dynamic models consider thalamic activity as an external input to the cortical dynamics. Here we review the main principles behind such models.

## Background and Motivation

In the context of motor computations, thalamus is often thought to have a special status that distinguishes it from the many sources of cortical input. Not only does the anatomy indicate robust thalamocortical projections (see **Section IV** of this volume), it also reveals that the signals transmitted by the thalamus are unlike those that could be received through other pathways. Specifically, the thalamus has access to sensorimotor inputs—through the superior colliculus (Crapse and Sommer, 2008), cerebellum (Caligiore et al., 2016), and various midbrain regions (Inagaki et al., 2022)—which can guide (pre)motor cortical dynamics faster than if this information had to be processed by other cortical areas first. This is supported functionally by studies that have revealed direct causal evidence for the importance of thalamic input in dynamic sensorimotor cortical processing (Crapse and Sommer, 2008; Guo et al., 2017; Sauerbrei et al., 2019; Inagaki et al., 2022).

Therefore, several models have been proposed to account for such thalamic input to (pre)motor cortical dynamics. In such models (Figure 34.3A), cortical dynamics are instantiated through a differential equation, which links ↳ an infinitesimal change in cortical activation per unit time $\frac{dh}{dt}$ to the sum of the external thalamic input $Ur$ and the cortical recurrent input $f(W, h)$. Therefore, these dynamics read $\frac{dh}{dt} = f(W, h) + Ur$, where $h$ and $r$ are the cortical activities and thalamic rates, $W$ and $U$ are the corticocortical and thalamocortical weights, and $f$ represents some arbitrary function. While the recurrent cortical weights are particularly influential in sculpting complex network dynamics due to their numerous degrees of freedom, the input can also play a non-negligible role, especially if the dynamics include a nonlinearity and the input is particularly strong.
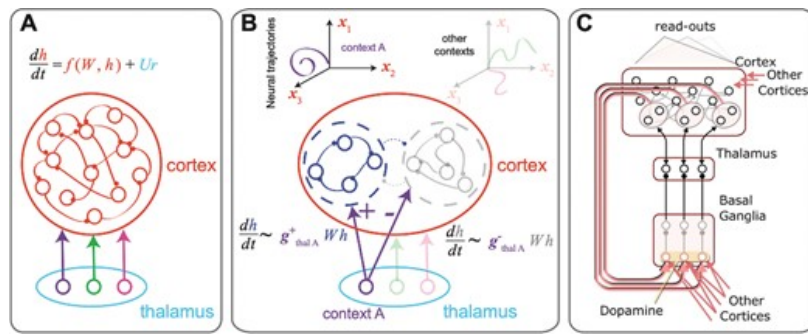
**Figure 34.3.** Type II models: thalamus as an external feedforward input to cortical dynamics. (A). General framework. (B). An example of an interaction between thalamic input and cortical dynamics (with a mechanism similar to Rikhye et al., 2018). Bottom: The thalamic input gates cortex by acting as a gain factor on the cortical neurons; i.e., the inputs to cortex from the active thalamic neurons operate as multiplicative factors that facilitate ($g^+$) and suppress ($g^-$) different cortical subpopulations. Top: If the thalamic input is context-dependent, then this mechanism allows the selection of specific neural trajectories dictated by the cortical neurons that are "gated in." (C). Example of a model adapted from Mannella and Baldassarre (2015), where basal ganglia-to-thalamus signals are proposed to select cortical dynamics.

In the following section, we will review the diverse roles that thalamic inputs have been shown to play in various models of Type II.

## Model Details

Considering neural dynamics—as opposed to a static cortical representation—can substantially alter the mechanisms of action of thalamus on cortex, even in models that remain closest to the representational type. For instance, Bachschmid-Romano et al. (2022) have proposed a model which is built to encode reach direction in a stable manner while constrained to mimic observed cortical activity. In this model, inputs to the cortex—putatively from thalamus—are not only tuned to the characteristics of the movement, as they would be in a Type I model. Rather, this model also includes "untuned" inputs—especially during the movement period—that help shape activity patterns that are shared across movements despite their separate characteristics (Bachschmid-Romano et al., 2022).

The roles that thalamic input can play become even more diverse when moving further away from a fixed representational perspective. For instance, cortical network dynamics are thought to participate in updating representations of the external world to compensate for self-generated movements (Crapse and Sommer, 2008). A feature of this computation is input from thalamus that reflects an "efferent copy"—a broadcast of the motor command. The evidence for such a mechanism has perhaps been strongest for the update of visual representations in response to eye movements, where the mediodorsal (MD) nucleus of the thalamus has been shown (Crapse and Sommer, 2008) to receive saccade-related information directly from the superior colliculus (the putative origin of the motor signal). The MD thalamus then transmits this saccade information to the frontal eye field (Crapse and Sommer, 2008), where it can be integrated with visual information through recurrent dynamics. This mechanism has indeed been successfully implemented in a model of the type illustrated in Figure 34.3A (Rao et al., 2016).

Finally, models have also clarified how feedforward thalamic inputs can act as selectors or gates that can largely impact the activity of cortical circuits, even while their dynamics are largely driven by their internal recurrence. For instance, models have suggested that strong thalamic inputs can leverage the nonlinearity of the transfer function of cortical neurons, therefore modulating their response to cortical recurrent inputs through an effective gain (Figure 34.3B; Rikhye et al., 2018; Stroud et al., 2018). This gain modulation can be pushed to an extreme such that the thalamic input can act like a gate that selects particular cortical subpopulations that will then implement specific dynamics. In such cases, the gain causes relatively large recurrent interactions in some populations while "extinguishing" others through near-zero gain. Such a mechanism was, for instance, proposed in a model of premotor computations, where context-selective thalamic units facilitated cortical context-dependent processing of sensory cues through gating, thereby leading to the correct context-dependent action (Rikhye et al., 2018). Another model where thalamus acted as a gate for cortical subpopulations was implemented in Calderon et al. (2022). Here, in the context of movement sequences, thalamus was

used to select the next premotor cortical subpopulation—which indexed a particular movement—in response to basal ganglia activation. Finally, in Mannella and Baldassarre (2015), a basal ganglia–thalamus input pathway was modeled similarly to Rikhye et al. (2018), by gating out irrelevant recurrent subpopulations while selecting and modulating relevant ones that then drive the motor output—putatively through dynamic attractors in the activated cortical subpopulation (Figure 34.3C).

## Limitations of the Approach and Relation to Other Models

A limitation of Type II models is that they either fully omit the feedback connections from cortex to thalamus, or do not leverage and explain the specific advantages of the striking thalamic architecture—which is characterized by the absence of local excitation (see **Section II** of this volume) and the presence of long-range bidirectional interactions with the cortex (see **Section IV**). Therefore, in these models, there is no conceptualization of specific computational benefits arising from thalamic processing beyond relaying information from the thalamic afferents.

# Type III Models: Thalamocortical Loops Reconfigure Cortical Dynamics

We now turn to Type III models (Kao et al., 2021; Logiaco et al., 2021; Shine, 2021; Lakshminarasimhan et al., 2022; Recanatesi et al., 2022), whose development was spurred by recent experimental evidence from simultaneous recordings in motor cortex and thalamus and optogenetic perturbation studies (Guo et al., 2017; Sauerbrei et al., 2019). The distinction of these models is that the loop between cortex and thalamus—including the feedback projection from cortex to thalamus in addition to the more well-studied connection from thalamus to cortex—plays a crucial computational role (Kao et al., 2021; Logiaco et al., 2021). Additionally, the synaptic weights in the loop—upon which its computational capability depends—can be set via biologically plausible learning (Lakshminarasimhan et al., 2022). These models demonstrate how thalamocortical loops can remap cortical dynamics to influence behavior. In contrast, for Type I and II models, only the feedforward connection from thalamus to cortex is considered. This difference imbues Type III models with much richer ability to control and sequence movements.

We will expand on this below, but it is important to clarify this crucial distinction immediately. An input to a recurrent neural network (i.e., thalamus to cortex, as in Type I and II models) has a limited capability to impact dynamics. Loops that are bidirectionally coupled to a recurrent network, on the other hand, if their synaptic weights are appropriately tuned, can radically remap network dynamics due to their impact on the recurrent structure itself (Figure 34.4A). As we shall see, this distinction has deep computational implications and thus Type III models make claims about the role of thalamocortical interactions in motor control that differ qualitatively from prior theories. It is important to note that these feedback loops may be polysynaptic (e.g.,

originating from and returning to different cortical layers; see **Sections II and III** of this ↳ volume), but this detail does not alter the computational characteristics of these models.
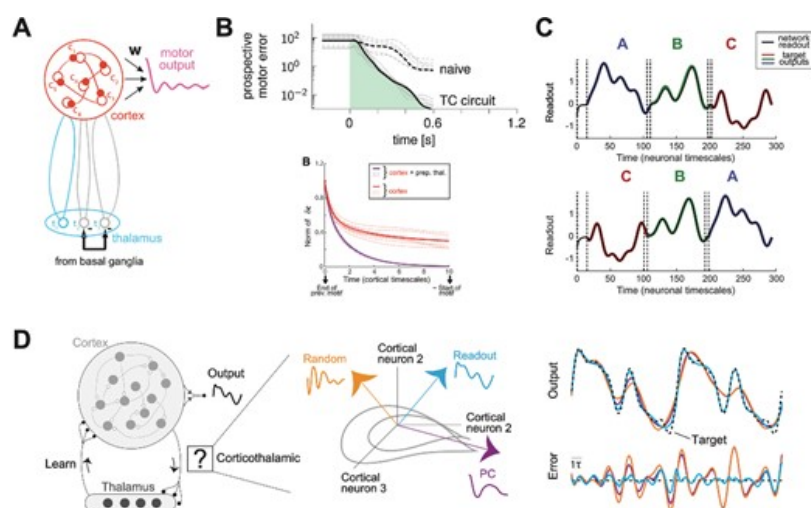
**Figure 34.4.** Thalamocortical interactions as loops between cortex and thalamus. (A). The basic structure of Type III models in which feedforward connection to cortex and feedback connections to thalamus are both essential. (B). Kao et al. (2021) (top) and Logiaco et al. (2021) (bottom) use thalamocortical loops to instantiate cortical dynamics that permit much more rapid motor preparation than is possible with simple feedforward input. (C). By switching between thalamocortical loops used for motor preparation and motif-specific execution, Logiaco et al. (2021) show that motor sequences can be strung together in arbitrary orders. (D). Lakshminarasimhan et al. (2022) identify conditions under which biologically plausible learning of thalamocortical synaptic weights results in the motor output matching a target function even when the size of the thalamus is small relative to cortex. Successful motor learning occurs if the corticothalamic projection is aligned to the motor readout direction (blue). If the projection is instead aligned to the principal component (PC, purple) directions of the cortical activity, or if the corticothalamic weights are random (orange), then thalamocortical learning is substantially worse. Tau ($\tau$) denotes neuronal time constant. A, B (bottom), and C are adapted from Logiaco et al. (2021); B (top) from Kao et al. (2021); and D from Lakshminarasimhan et al. (2022).

# Background and Motivation

## Experimental Data for the Importance of Thalamocortical Loops

The validity of the critical loop structure in Type III models is motivated by both anatomical and functional findings. With respect to the former, projections to and from the same population of motor cortical neurons can connect to the same populations of thalamic neurons. In other words, cortex and thalamus form a loop (see **Section IV** of this volume). Recent functional studies have demonstrated that these loops are required for many cognitive and motor functions (Guo et al., 2017; Rikhye et al., 2018; Sauerbrei et al., 2019) and that inhibiting higher-order thalamus suppresses cortical activity, while inhibiting cortex impacts thalamic activity (Guo et al., 2017). Together, these results provide strong experimental evidence for the importance of the looped nature of thalamocortical interactions in motor control, rather than a largely feedforward circuit in which the feedback from cortex to thalamus plays at most a limited role, as in Type I and II models.

## Theories Conceptualizing the Role of Thalamocortical Loops in Motor Dynamics

Recently, a few theoretical frameworks have emerged that can generate specific hypotheses about how the highly stereotyped thalamocortical loop architecture facilitates motor control. To be analytically tractable and yield robust insight, these frameworks rely on the simplification that the dynamics in the cortex-thalamus system are linear or switching linear (Glaser et al., 2020). While this may seem unrealistic at first blush, in the context of the dynamics of primary motor cortex specifically, this simplification appears to be largely reasonable given that cortical population activity has been shown to be well captured by shared linear dynamical systems for whole classes of movements (Lara et al., 2018; Glaser et al., 2020).

One such framework is optimal control theory, an elegant approach that aims to find the best possible input to a dynamical system—such as a cortical network—so that it evolves according to some desired specification. A power of this framework is that—under some conditions—the optimal input can be identified analytically and, furthermore, can be implemented through feedback loops similar to those between the thalamus and cortex (Kao et al., 2021). The idea that the computational role of thalamocortical interactions in the production of behavior is optimal feedback control is novel and intriguing. A limitation of this framework is that it is unclear how to augment the goal of optimization with other desirable features such as robustness to (unpredictable) variability in this goal or in the dynamics of the system, though steps have been made in this direction outside of standard optimal control (Loeb, 2012; Eysenbach and Levine, 2022). Additionally, with respect to the thalamocortical system per se, integrating the smaller size of the thalamic population relative to the cortex is not straightforward.

Another framework of interest—which proposes a functional role for the relative sizes of a large cortex and a small thalamus—follows from the fact that the cortex-thalamus system can be conceived of as "full-rank" recurrent connectivity in the cortex, modified by "low-rank" connectivity through the thalamus. Concretely, for a population of $N$ cortical neurons, the $N \times N$ synaptic weight matrix $W$ describes the (full-rank) recurrent connectivity. We can then define 2 $N \times K$ matrices $U$ and $V$ which represent the thalamocortical and corticothalamic synaptic connectivity, respectively, with $K \ll N$. The dynamics of the cortex-thalamus system are thus governed by $W + UV^T$, a low-rank modification of $W$.

This conceptualization connects to a body of recent work that has explored the computational features of low-rank additions to full-rank synaptic weight matrices and their application to neuroscience. These studies have shown that in some settings, desired network computations can be realized even if only the low-rank component is structured (Mastrogiuseppe and Ostojic, 2018). Furthermore, when the weights of the low-rank component $UV^T$ are learned in a way that accounts for the full-rank $W$, this can substantially reconfigure network dynamics. Relating to the thalamocortical system explicitly, a synergy between cortico-cortical and cortico-thalamo-cortical weights can facilitate solving complex tasks that would otherwise be intractable if these two populations of synapses were uncorrelated (Schuessler et al., 2020a; Logiaco et al., 2021). Moreover, other studies have shown that learning in recurrent neural networks often only induces low-rank changes in recurrent weights (Sussillo and Abbott, 2009; Schuessler et al., 2020a; Schuessler et al., 2020b; Susman et al., 2021; Feulner et al., 2022). While this framework has the advantage of being flexible, it also has specific limitations, including an assumption that the thalamic units respond rapidly relative to cortical dynamics, and its analytical characterization is not as complete as in the case of the optimal control framework.

Note that both of these frameworks emphasize that the computational benefit of thalamocortical loops is achieved through specific tuning of their synaptic weights, which opens up the question of the types of learning rules that are involved in that process.

## Model Details

### Thalamocortical Loops for Motor Preparation

As discussed above, a posited role for the motor cortex is the internal generation of dynamics that participate in driving the musculature during movement. Studies have shown that the evolution of the cortical activity during a ballistic movement (e.g., an arm reach to the left or the right) is highly dependent on the "initial state"—i.e., the neural activity immediately prior to movement onset—and that variability in the initial state is reflected in variability in the behavior (Churchland et al., 2006). These results suggest that an important part of motor control is "motor preparation"—the computation of correctly identifying and setting the initial state.

Recent studies, including Logiaco et al. (2021) and Kao et al. (2021), have proposed Type III models that explore how thalamocortical loops can prepare motor cortex and then trigger movement onset. These models share the mechanism that loops between cortex and thalamus with appropriate synaptic weights can force the cortical activity—despite starting in an arbitrary configuration—to evolve to a desired initial state with much greater rapidity than is possible when driving the cortical network with an isolated external input (i.e., as in Type I and II models; Figure 34.4B). After preparation, movement execution in both models can proceed with negligible error.

In Kao et al. (2021) the authors use optimal control theory to analytically identify thalamocortical loop weights that will drive network activity to configurations that minimize movement errors following preparation. This indirectly results in network dynamics that evolve to correct initial states. Interestingly, they show that only a small number of directions in neural activity space are important for guaranteeing successful motor outputs. Consequently, there is a volume of activity space within which all configurations are valid initial states for a given movement. In alignment with this finding, the solutions the authors derive generate control signals that selectively eliminate errors along the relevant dimensions.

Logiaco et al. (2021), on the other hand, directly finds the synaptic strengths of thalamocortical loops that decay cortical activity as quickly as possible to the initial state that will lead to accurate movement. Of note, in contrast to Kao et al. (2021), this approach does not find solutions that selectively ignore the directions in activity space that are irrelevant for the upcoming movement. On the one hand, this has the disadvantage of performing less optimally when the dynamics during movement execution are shared across movements. However, on the other hand, this leads to thalamocortical loops that can perform robustly across the multiple distinct execution dynamics that are associated with different neural activity subspaces, each supporting specific classes of movements. In addition, while direct optimization loses the connection to the elegance of optimal control theory, advantages include the ability to identify loop weights directly in nonlinear networks and to impose size constraints on the thalamocortical circuit such that the thalamus has many fewer neurons than the cortex (Logiaco and Escola, 2020).

## Thalamocortical Loops for Motor Execution and Sequencing

An important problem in motor control is the generation of sequences of varied movement building blocks, or "motifs" (Merel et al., 2019). Important features of this computation include flexibility—stringing motifs together by successfully transitioning between them in any arbitrary and potentially novel order—and extendability—learning new motifs without impacting previously acquired ones. Complicating this problem is the fact that an individual motif may have timescales (i.e., its duration and frequency content) that differ considerably from other motifs. In consequence, a fixed cortical dynamical model may fail to generate all of these motifs without a mechanism to powerfully and flexibly reshape its dynamics. While learning in the motor cortex can potentially allow it to generate motor outputs with certain timescales, this comes at the cost of potentially overwriting prior learning and decreasing the performance for other outputs.

Logiaco et al. (2021) tackled this problem by proposing that—while the cortical connectivity provides a "prior" over the dynamics that may be relevant for the execution of a variety of movements—different thalamocortical loops could be instantiated to support the dynamics needed for specific classes of motifs. It was shown analytically that such loops—which act as low-rank perturbations to the cortical network—can be constructed such that the necessary timescales are guaranteed to exist in the dynamics of the cortex-thalamus system (i.e., $W + UV^T$). Moreover, the thalamocortical loop weights can be tuned to prevent noise accumulation along the direction relevant for movement such that individual motifs can be executed robustly without unrealistic precision in the initial, pre-movement network activity. When combined with the model for fast motor preparation (described above), this permitted the elaboration of arbitrary sequences by switching between thalamocortical loops for motif execution and preparation (Figure 34.4C). It was further shown that the thalamocortical architecture is relatively efficient as it can mitigate the size of the neural networks needed in generating these complex and varied motor sequences.

This study proposed that the basal ganglia could implement the selection of motifs. The basal ganglia provide strong ↳ inhibitory input to the thalamus whose pattern changes at the transitions between movements. This suggests that the basal ganglia could "play the thalamic piano" by successively turning on and off different thalamocortical loops to instantiate the different dynamics needed to prepare and execute a sequence of motifs. In this way an abstract sequence code—represented in the basal ganglia output—is converted to a motor pattern that can drive behavior through the dynamics of the cortex-thalamus system.

Another study has specifically explored the computation of sequencing at the premotor level (Recanatesi et al., 2022). In this study, thalamocortical interactions implement context-dependent selection of sequences of cortical states. This model demonstrates that the recurrent cortical connectivity can define different quasi-stable population activity patterns whose activation is sustained through recurrent excitation. Then, a few specific thalamocortical loops acting as a low-rank perturbation to the cortical network can interact with the intrinsic cortical dynamics to drive switching through a sequence of such patterns. The model shows that the properties of

the thalamocortical connectivity can shape not only the right sequence order, but also the correct variability in activation time for each cortical population pattern.

## Biologically Plausible Learning in Thalamocortical Loops

The models we have just discussed show that it is possible to perform computations by tuning synaptic weights in cortico-thalamo-cortical loops appropriately, but these models have not addressed how the loop synapses can be updated with biologically plausible learning. Several such approaches have been proposed for credit assignment in recurrent networks (Gilra and Gerstner, 2017; Murray, 2019), but a recent study showed that biologically plausible learning is only effective for updating thalamocortical—but not corticothalamic—synapses (Lakshminarasimhan et al., 2022). To resolve this challenge, a model was developed in which structured corticothalamic connectivity—proposed to emerge over evolution and to be independent of any specific motor task—was shown to dramatically enhance learning in thalamocortical synapses. Specifically, the corticothalamic pathway needed to communicate an efferent copy of the motor command (Figure 34.4D).

Supporting this, corticofugal projections are known to send axonal branches to the thalamus (Bourassa et al., 1995; Kita and Kita, 2012; Sherman, 2016) while also targeting lower motor centers (Guillery and Sherman, 2011). Furthermore, a reanalysis of neural data from Sauerbrei et al. (2019) confirmed that the alignment of the activity of thalamic neurons with the cortical motor output was significantly greater than chance during a pellet-grasping task (Lakshminarasimhan et al., 2022).

This study provides important support for the validity of Type III models by demonstrating both that the loop weights which underlie their function can be learned in a biologically plausible way and that aspects of corticothalamic connectivity upon which the model relies are observed anatomically and functionally in extant data.

# Conclusion

In this chapter, we have reviewed models of thalamocortical interactions in motor control through the lens of their assumptions about the functional relevance of primary motor cortical dynamics during movement, as well as the feedforward versus recurrent aspect of thalamocortical interactions (Figure 34.1).

Given the recent experimental results demonstrating the relevance of fine cortical dynamics to drive at least certain types of movements (Shenoy et al., 2013; Sauerbrei et al., 2019; Guo et al., 2021), we have argued in this chapter that the recent modeling developments showing how recurrent thalamocortical loops can reconfigure cortical dynamics are particularly relevant to shed light on the mechanisms by which thalamocortical interactions can serve motor control. In particular, these models can inspire new analyses and experiments to further test the mechanisms they propose. In a general sense, the Type III models discussed here suggest the importance of bidirectional interactions between thalamus and cortex. While there has been a recent validation of the importance of thalamocortical inputs for motor cortical dynamics (Sauerbrei et al., 2019), to the best of our knowledge more progress remains to be made for testing whether the corticothalamic projections can significantly affect motor thalamus activity. In addition, several models assume that different thalamocortical loops are associated with different types of behaviors or different stages of a task—assumptions that remain to be fully tested. Similarly, as is always the case when considering the importance of structured connectivity, a confirmation of the mechanisms by which thalamocortical interactions may be tuned through experience-dependent learning awaits experiments that are able to monitor these phenomena with the appropriate resolution.

Finally, there are also several open avenues for building further on current thalamocortical models. In particular, there is currently little understanding of the synergistic interactions between different cortical regions and different thalamic nuclei during motor control. Therefore, we expect that this line of research will continue to provide valuable insights to the field of thalamocortical interactions.

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