

Top-Down Executive Control Drives Reticular-Thalamic Inhibition and Relays Cortical Information in a Large-Scale Neurocognitive Model

M E Phillips,¹ M C Avery,² J L Krichmar,² R Bhattacharya¹

¹HRL Laboratories LLC & ²Department of Cognitive Sciences University of California, Irvine

Abstract

The thalamus is a critical brain structure involved in gating and regulating the flow of sensory and cortical information. The reticular nucleus of the thalamus (TRN) sends inhibitory projections to the thalamic relay nuclei instead of projecting to the cortex as the other thalamic nuclei do. These inhibitory projections endow the TRN with the functionality to modulate and control cortical information flowing through the thalamus. Yet, the functional roles of the TRN and thalamus in high-level cognitive processing, such as spatial reasoning and decision-making, remains poorly understood. Neurocognitive models offer a framework to explore the high-level cognitive functions of the thalamus and TRN. Here, we investigate the functional roles of the thalamus and TRN in high-level cognitive tasks using a large-scale neurocognitive model called ICArUS-MINDS. Our results demonstrate distributed and parallel top-down executive control of semantic and spatial cortical information. Specifically, we observed reticular-thalamic inhibitory gating of spatial and semantic information through top-down task switching control during reasoning, decision making and recall. Thalamic-gating was critical for orchestrating processing sequences of task-dependent switches between cortical sources and targets. These results are an important first step in simulating and understanding the functional roles and behaviors of the thalamic brain system in high-level cognitive processing.

Introduction

Neurocognitive models of top-down executive control and gating typically employ direct connections or local network dynamics as the fundamental modulatory mechanisms (Herd et al. 2006; Matthews and Mackintosh 1998). However, the human brain is known to utilize relay circuits between the thalamus and the cortex as one of the primary mechanisms for regulating top-down executive control (Guillery & Sherman 2002). Models incorporating thalamic relay circuits have been primarily used in investigations of the top-down modulation of sensory stimuli, notably spatial attention (Shipp 2004). However, the functional roles of the thalamic relay circuits in *higher-level* cognitive processing remains unexplored due to limited experimental and modeling investigations.

Recent experimental work has elucidated the spatial topography and connectivity of the high-level thalamic relay circuits (Saalman et al. 2012; Zikopolous & Barbas 2006; 2007). These results allow neurocognitive models to accurately simulate and study the features and functionality of thalamic relay circuits. Some features beneficial for cognitive models include: brain-region specific networks consisting of a small number of nodes, and supporting distributed computations and parallel processing (Briggs & Usrey 2009). Together, these studies also showed that the functions of the thalamic relay circuits are modular and generalizable, allowing their potential application to benefit many neurocognitive models.

Here, we describe simulations of high-level thalamic circuits within a large-scale neurocognitive model. The ICArUS-MINDS neurocognitive model simulates human behavior in complex geo-spatial intelligence tasks utilizing top-down task switching, spatial estimation and reasoning, and semantic decision making and recall. The model is comprised of neural network layers connected by synaptic weights, which are trained for task-specific applications. Here, we demonstrate parallel top-down gating of cortical information through thalamic relay circuits in three high-level spatial reasoning and decision making tasks.

Neurobiological Background

The thalamus is a central brain structure and critical for gating and regulating sensory and top-down executive control. First and high-order thalamic relays circuits consist of excitatory feedforward and feedback loops connecting thalamic relay neurons to corresponding cortical areas (Guillery & Sherman 2002). First-order thalamic nuclei receive sensory input and relay this information to the cortex. High-order thalamic nuclei (e.g. medial-dorsal (MD) and Pulvinar) contain the majority of the thalamic relays. High-order thalamic relays are organized non-reciprocally in a top-down hierarchy, and relay executive information from one cortical region to another (Guillery and Sherman 2002; McFarland and Haber 2002).

However, a critical thalamic nucleus, the reticular thalamic nucleus (TRN) envelops the other thalamic nuclei and sends inhibitory projections directly to them. These inhibitory projections endow the TRN with the

functionality to gate information through first and high-order thalamic relays. This functionality is exploited by top-down executive control signals from the pre-frontal cortex (PFC) through the modulation of reticular inhibition/disinhibition of the thalamic relays (see Fig. 1, Guillery & Sherman 2002).

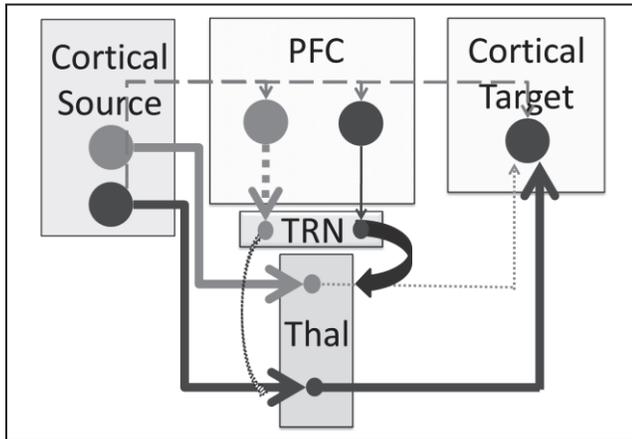


Figure 1. Neurobiological circuit architecture of the relay (Thal) and reticular (TRN) thalamic systems. Two cortical sources (dark and light) compete for the same cortical target. Executive top-down control from the PFC excites units in the TRN which map to the thalamic relays of cortical sources. Dis/inhibition of the thalamic units from the dark/light TRN units (curved lines) functionally opens/closes the source to target gate (open relays=solid line, closed relay=dotted line, corticocortical connections=dashed lines).

Functionally, this means that executive signals can gate and modulate parallel information channels relayed to distributed cortical regions via the TRN (see Fig. 2). Cognitively, executive regions can utilize this mechanism to provide a top-down contextual (i.e. a learned and task-specific) modulation of spatial and semantic information during reasoning and decision making.

Drawing from these results, we created biologically-realistic neural models of the thalamus and TRN which accurately reflect the topography of the input and output circuit connections. These component models were integrated into a large-scale neurocognitive model to examine the cognitive implications of these neural circuits and their architecture within a realistic and functioning network. Here, we show that top-down modulation of the thalamic relay circuits is critical for orchestrating cortical-processing sequences of cognitive task switching control during spatial reasoning and decision-making.

Materials & Methods

The ICaRUS-MINDS Neurocognitive Model

The thalamus and TRN component models were created to investigate biologically-realistic mechanisms for top-

down gating of competing inputs to cortical layers within the large-scale ICaRUS-MINDS model (see Fig. 3).

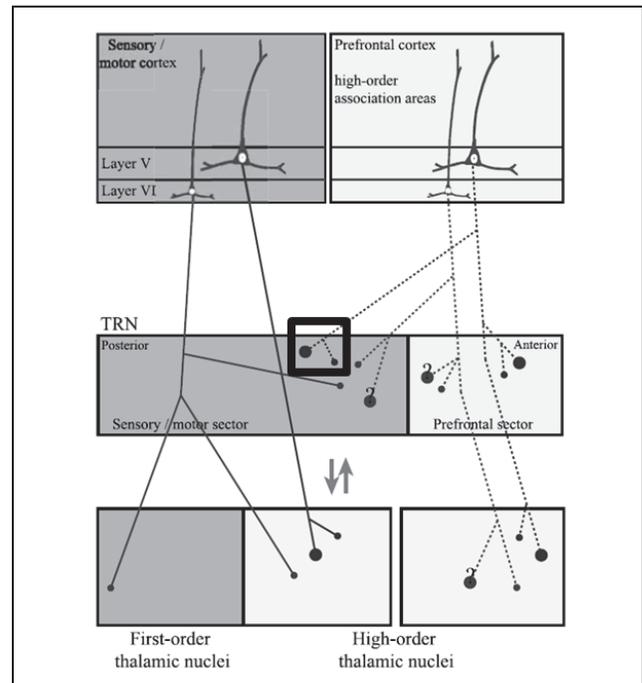


Figure 2. Top-down non-topographic modulation of TRN inhibition to thalamic relay nuclei is indicated by the black box (modified from Zikopoulos and Barbas 2006).

The model simulates nine major brain regions (PFC, anterior cingulate cortex (ACC), orbital frontal cortex (OFC), parietal cortex (PC), temporal cortex (TC), basal ganglia, hippocampus, brainstem, and the thalamus), and was constructed to perform six spatial-reasoning and decision making tasks for the COIN-AHA challenge problem in IARPA's ICaRUS program (COunterINsurgency Abducting Hot-spots of Activity, see MITRE 2013a,b for a detailed description). Briefly, in tasks 1-3 spatial reasoning is required to estimate the likelihood of an attacking group from a spatial pattern of prior attack locations. In tasks 4-5, the attack probabilities of the groups must be updated from new intelligence information, and in task 6 semantic decision making is required to select amongst intelligence reports. The ICaRUS-MINDS model must perform these cognitive actions, and switch between these tasks. The overall goal of the program is to understand human cognitive biases through neurally-accurate brain models.

Neural Simulations

The neural simulations used in this work are based on the Leabra framework in the Emergent simulation software, described in (O'Reilly & Munakata, 2000) and can be downloaded here: (http://grey.colorado.edu/emergent/index.php/Main_Page).

Emergent is a full-featured neural network simulator descended from PDP and PDP++. Emergent primarily supports complex, and multi-regional brain models (see Aisa et al. 2008 for a detailed description).

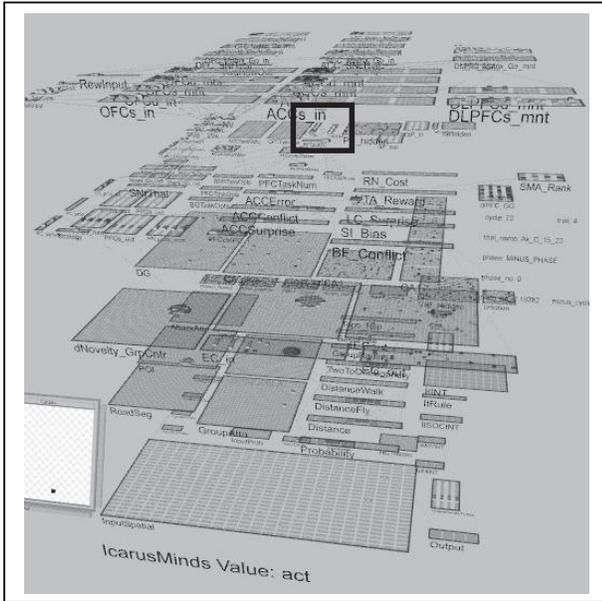


Figure 3. The nine brain region ICarUS-MINDS neurocognitive model (thalamus & TRN components are highlighted by the box).

Within the Emergent simulator, neurons summate excitatory, inhibitory, and leak conductances into a membrane potential that is thresholded and passed through a sigmoidal function to produce rate coded outputs. Layers in the model use ensembles of excitatory neurons with k-winner-take-all inhibition to simulate both populations efficiently. Learning is accomplished through a mix of Hebbian and error driven learning that incorporates an adaptive threshold for firing. The model operates in 2 phases: a minus phase where only input stimuli are clamped onto input units (with no synaptic modification), and a plus phase where both input and output units are clamped (i.e. allowed to fire). Differential neural activations from the 2 phases drive error driven learning. Connections between layers can follow a variety of topologies, including one-to-one, full, and geometric to create specific receptive fields. Figure 4 shows how the general architecture from Figure 1 was adapted in the ICarUS-MINDS model to accomplish three applications of task switching control, spatial reasoning, and semantic decision making and recall (see Applications of the Cognitive Architecture).

Results

Neurocognitive Features & Mechanisms

The ICarUS-MINDS model required an architecture to allow the PFC layer to appropriately gate competing cortical information paths by directing the appropriate inputs to relevant layers, and gating irrelevant inputs. Here, we describe the neural features and mechanisms, including the projections, size, inputs and outputs of the relay thalamus and TRN layers, implemented to achieve functional top-down gating in the ICarUS-MINDS model.

Gating Mechanism: Functional gating is produced by adjusting the relative weights of the connection strength between the source and target layers by the thalamus. The thalamic unit activations causing these adjustments are trained within the network through supervised error and Hebbian driven learning of the task-specific control signals. The inhibitory connection weights in an all-to-all projection between the TRN and thalamus learn to translate executive top-down signals into a thalamic activation pattern which maps to the cortical connection topography (see Fig. 4). The relative weights of the specified cortical connections are then adjusted dynamically, as the model runs. This adjustment can be either facilitating or silencing (Logothetis et al. 2010). In training, the network began with random layer activation with a sum of squared-error of prediction (SSE) of 0.144, after 20 epochs of training; the network reached an SSE of 0.007.

Network Inputs & Outputs: As depicted in Figure 4, the thalamus and TRN layers receive top-down excitatory control signals from PFCTaskNum layer (a task-specific control signal: 1-6). The PFCTaskPhase layer sends excitatory input to TRN units that specify a sub-phase within a task (see Applications of the Cognitive Architecture: Application 3). This non-topographic top-down control signal results from layer 5 pyramidal neurons in the PFC distributing projections widely to both PFC and non-PFC regions of the TRN (see box in Fig. 2, Zikopoulos & Barbas 2006; 2007). These executive signals convey a task-specific context for relative-weight connection strength adjustments. Under control by the PFC layer, the thalamus and TRN layers provide a functional gate for inputs to the Probability and Distance layers in the PC and EC_in layer in the hippocampal system (the Probability layer stores an online estimate of a group's attack likelihood, and Distance contains an estimate of the spatial separation between a group and an attack location). Inputs to these target layers are mutually exclusive (except for the EC_in during task 6, where two inputs occur during two separate hippocampal-phases, see application 3 and Fig. 4).

Connection Topography: The cortical projections of the thalamic relay circuits are organized with a topography reflecting the thalamocortical projections to DistanceFly, DistanceWalk, PCProbsOut and VIPHidden in the PC and

ITINT, ITRule, and Group_ID in the TC (See Fig. 4 and Applications of the Cognitive Architecture for a detailed description of these layers and their cognitive functions, Behrens et al 2003; Schmahmann & Pandya 2004). The TRN layer is organized with a local topography that reflects the top-down inputs from PFCTaskNum and PFCTaskPhase. This mixed PFC/PC topography in the thalamic system is seen in high-order associational thalamic nuclei (such as MD and the Pulvinar, Guillery & Sherman 2002; Zikopoulos & Barbas 2006; 2007). This input/output architecture of the thalamus and TRN is believed to be a central mechanism for top-down executive control (Zikopoulos & Barbas 2006).

Network Size: The thalamic layers consist of a seven unit (rate-code based neuron ensembles) relay thalamus and an eight unit TRN, each of which maps to a functional domain, and internal to each is a population of neurons (see Fig. 4). The extra unit in the TRN is required for task-phase switching described in Application 3. In addition, these layers maintain a realistic ratio of thalamic to cortical neurons in ICaRUS-MINDS (~1:160 Williams & Rakic 1988; O’Kusky & Colonnier 1982), while maintaining a large information bandwidth between cortical areas.

Cognitive Architecture Comparison: The ICaRUS-MINDS model, created to simulate neural structures and their functions, shares common features with many cognitive-architectures such as working, semantic, and episodic memory systems, a biased-competition based attentional system, as well as reward, error, and Hebbian learning systems (see Samsonovich 2012, BICA table for a detailed comparison with other cognitive architectures). Numerous differences also exist. For example, ACT-R has used a recency code in episodic memory for a similar task switching behavior (Altmann & Grey 2008).

Neurocognitive Model Performance

The ICaRUS-MINDS neurocognitive model performance was compared to the average behavior of 103 humans in probability prediction (S1) and resource allocation (S2). The model matched human behavior well in tasks 1,3,5, and 6 (0=perfect match, 1=poor match, see Table 1 and MITRE 2013a for details).

	Task 1	Task 2	Task 3	Task 4	Task 5	Task 6
S1 (H-M)	-0.0118	0.1208	0.0477	0.1180	0.0523	0.0639
S2 (H-M)	-0.0160	0.1256	0.1379	0.0359	-0.0147	0.0326

Table 1. ICaRUS-MINDS performance across all COIN-AHA tasks. S1 measures the model’s match to human reported probability values with respect to the Bayesian probability distribution (Human –Model probabilities). S2 measures the model’s match to human’s resource allocation behavior (Human –Model Resource allocation; see MITRE 2013a, b for tasks and score details).

Applications of the Cognitive Architecture

This section details three applications of the thalamus and TRN models fully-integrated into the ICaRUS-MINDS neurocognitive model for the COIN-AHA challenge problem. This complex geo-spatial intelligence problem requires task switching control in all tasks, spatial reasoning in task 1-3, and decision making in tasks 4-6 (see MITRE 2012a for a full description). In COIN-AHA, the model is required to estimate the likelihood of attacking groups from a spatial pattern of attack locations and intelligence reports. Here, we demonstrate that the thalamus and TRN models orchestrated multiple cortical sources and processing sequences to their cortical targets through top-down task switching control in three applications of high-level semantic decision making and spatial reasoning. These applications allow the architecture to use the same mechanism for top-down task switching control to gate cortical information based on task demands, and mix in recalled information for additional processing.

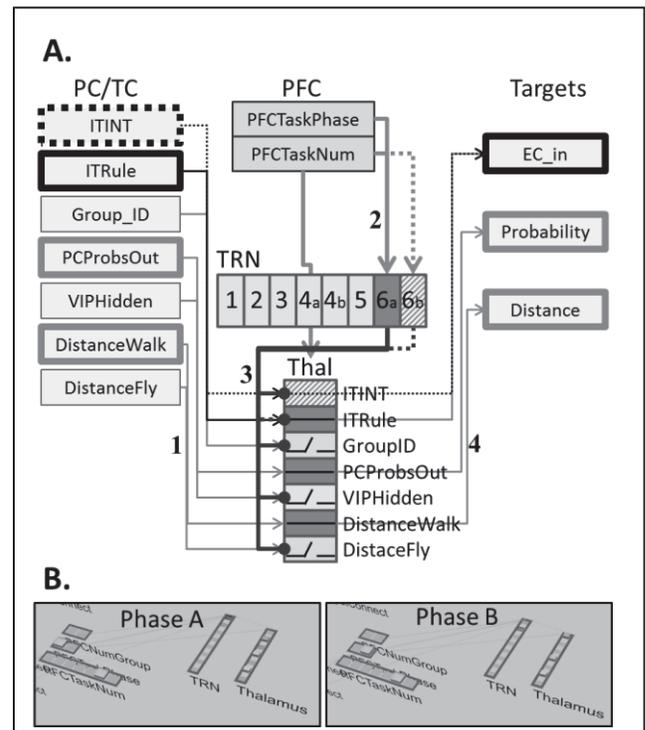


Figure 4. Multi-phase top-down gating of high-order thalamic relays during decision making. **A.** ITINT and ITRule project, via thalamic relays, to the EC_in layer. The TRN task 6a unit gates ITRule (solid line), the task 6b unit gates ITINT (dashed line). **B.** Examples of the circuit during phases A and B of task 6 in the ICaRUS-MINDS model. Dark filled/striped units are active–open gates, light filled units are inactive–closed gates (Connections: 1–one-to-one relay inputs, 2–one-to-one & one-to-all top-down executive modulation, 3–TRN inhibitory projections (learned), 4–one-to-one relay targets, black lines with circles=inhibitory connections, light lines with arrows=excitatory connections).

Application 1—Task Switching Control: The PFC provides executive top down control to direct the correct cortical information source to the correct cortical target region. This process is driven by task demands, and is mechanistically achieved through inhibition/disinhibition of the Thal layer by the TRN. The Probability layer within the PC uses two distinct inputs to estimate the probability of an attack (VIPHidden and PCProbsOut). VIPHidden is used in spatial reasoning to compute group attack probabilities from spatial parameters such as distance. In tasks 4-6, prior group probability values are given as inputs to the model and must be updated by additional intelligence information stored in PCProbsOut (Fig. 4).

Finer grained phasic task switching control is achieved in task 4 and 6 by using the 4a & 4b (6a & 6b) units of the TRN. This intra-task phasic switching is required during semantic recall and selection (see Application 3). The PFCTaskPhase layer provides an additional top-down excitatory input required to break the tie of equal excitation from PFCTaskNum between the two task phases. This additional input raises the correct unit above its activation threshold. The winner-take-all unit value of the TRN layer is manually set to one to ensure that only a single set of task and phase-specific connections are active at a time.

The thalamic units learn the correct relative-weight connection state (on/off) during network training as a function of the top-down executive signals of task and phase context (i.e. PFCTaskNum and PFCTaskPhase). For example, thalamic units 3 and 4 (counting from the bottom) adjust the relative weight connection strength between VIPHidden and PCProbsOut and the Probability layer respectively in Task 4. Without the TRN and thalamus layers updated probability information from VIPHidden does not reach the Probability layer in the PC. Any probability estimates after lesioning are sampled from a uniform probability distributed across all four options (25% each, after normalization).

Application 2—Spatial Reasoning: In the second application of the top-down thalamic gating circuit, two different spatial estimates of the distance between attack and group locations are gated into the Distance layer. DistanceFly is a 2D spatial representation of attack locations; DistanceWalk is a 1D road structure of attack locations. The Distance layer in the PC must receive input from only one of the layers to estimate the correct task-specific distance. DistanceFly is used in tasks 1 and 2, where Euclidean distances are estimated from the 2D space of attacks. In tasks 3-6, roads are present in the spatial pattern of attacks, and the distance from attack location to the group must be calculated along winding road segments using DistanceWalk. PFCTaskNum and PFCTaskPhase provide the task-specific top-down excitatory contextual inputs to the TRN which inhibit/disinhibit the corresponding units in the thalamus. The connection weights are learned as described in Application 1. The 1st and 2nd units in the

thalamus adjust the relative weights between DistanceFly and DistanceWalk to the Distance layer respectively. Without the TRN and thalamus layers, distance information cannot reach the PC and probability estimates can only be based on numerosity and radius.

Application 3—Semantic Decision Making & Recall: In the final application of the thalamic gating circuit, multi-phasic top-down control is applied to the recollection of semantic knowledge and in the decisional selection of intelligence reports. The hippocampal system is used in ICARUS-MINDS to recall and select the appropriate intelligence report to distinguish between groups. As depicted in Figure 4A, three TC sources (GroupID, ITINT and ITRule) are gated into the Entorhinal cortex (EC_in, the target layer), by the thalamus. In phase A of task 6 the intelligence rule (ITRule – a measure of the highest probability groups) is gated into EC_in to recall the semantic information contained within the different intelligence reports. Then, in phase B of task 6, the intelligence value (ITINT – a measure of semantic content) is gated into EC_in in order to select the appropriate intelligence report based on ITRule (see Fig. 4). GroupID is used to disambiguate attacking groups in tasks 1-3 when ICARUS-MINDS evaluates the probabilities for each group individually. As in the other two applications, the connection weights are learned, and PFCTaskNum and PFCTaskPhase provide top-down excitatory inputs to the TRN which inhibit/disinhibit the corresponding thalamic units. Without the TRN and thalamus networks, semantic recall is hindered and the model can only make random guesses to receive intelligence reports.

Discussion

We have demonstrated a biologically-accurate model of the thalamus and TRN that can functionally gate cortical information in a neurocognitive model of task switching control, spatial reasoning and semantic recall and decision making. Our model accomplished top-down executive control of high-order thalamic relay circuits through TRN-mediated inhibitory gating. The thalamic and TRN systems were an integral component of the ICARUS-MINDS neurocognitive model. This model accurately simulated many interacting brain systems and was an ideal framework to explore a *neural* model of top-down task switching control using the reticular-thalamic system (MITRE 2013a). The neural mechanisms of executive control of distributed, parallel cortical computations were critical for cognitive task sequencing of spatial reasoning, semantic recall, and decision making in the ICARUS-MINDS model.

This cognitive functionality was accomplished in a network with a large information bandwidth, and of biologically-accurate size and connectivity. The thalamic and TRN networks were essential to orchestrate task-

specific top-down control of cortical processing sequences in the PC and EC during high-level semantic decision making and spatial reasoning. Corticocortical connections, offer an alternative mechanism for this behavior (Sherman and Guillery 2011). However, the thalamic architecture described here can be easily adapted to many cognitive models requiring distributed executive control of parallel information channels from a small network. This architecture can also scale rapidly for many different tasks, requiring only one additional thalamic unit for each additional switch. Furthermore, this model provides an opportunity to examine the underlying causes of behavioral deficits from differences in cortical information processing due to PFC dysfunction in executive control.

One alternate theory suggests that top-down executive gating may be accomplished through spike synchrony or gamma oscillations in the brain (Minlebaev et al. 2011). Although the circuits presented here are functional analogs of the dynamical spiking mechanisms, our rate coding approach has a limited ability to capture spiking dynamics. Yet, a rate coding modeling approach has several advantages, such as binding and sequence maintenance (O'Reilly et al. 2003). Further work is required to contrast dynamical spiking with rate coding mechanisms, extend the role of the thalamus in other cognitive tasks, and to explore the role of attention and adaptation in regulating top-down control.

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