Title:

Corticostriatal Function in Sentence Comprehension: Insights from Neurophysiology and Modeling

Authors:

Peter Ford Dominey[1, CA], Toshio Inui[2,3]

1. CNRS & University of Lyon, 69676 Bron Cedex, France, peter.ford.dominey@univ-lyon2.fr

2. Department of Intelligence Science and Technology, Graduate School of Informatics, Kyoto University, Kyoto 606-8501, Japan, inui@i.kyoto-u.ac.jp

3. ERATO Asada Project, Japan Science and Technology Agency

Abstract

The characteristic organization of cortex, basal ganglia and thalamus can be considered a "canonical" macro-circuit of the primate brain. The intact function of the system requires intact function at the different nodes of the circuit. Cortico-striatal circuits are compromised in Parkinson's disease due to progressive loss of dopamine-producing neurons in the basal ganglia. Among the cognitive deficits observed in Parkinson's disease is an ensemble of perturbations in language processing, thus implying a role for basal ganglia in language processing. Related studies have suggested that basal ganglia dysfunction results in a more general deficit in certain forms of rule-based processing. From a functional neurophysiology perspective, neuro-imaging studies reveal activation of the striatum in diverse aspects of language processing including syntactic comprehension.

We present a model in which the unique capacity for the striatum to integrate functionally related cortical inputs is exploited for language processing. Converging cortico-striatal connections provide a mechanism that binds cortical representations of syntactic context in BA47 to structure mapping representations (corresponding to grammatical constructions) in BA44. This allows the retrieval of the appropriate grammatical construction to BA44 via thalamo-cortical connections, where it is subsequently used to perform the structure mapping. In this model, the rule retrieval function of the cortico-striatal systems is not unique to language. The model is evaluated in the context of behavioural and neurophysiological results from basal ganglia dysfnction. Likewise, as the model makes strong assumptions about the cortical and subcortical neuranatomy, recent results in human neuroanatomy are reviewed in the context of these assumptions.

1. Introduction

One of the outstanding open issues in neuroscience concerns the functional significance of the neuroanatomical organization of the primate cortico-striatal system, and its role in human cognition. In a highly influential review article based on extensive studies of primate neuroanatomy, Alexander et al. (1986) described the organization of the massive projections from neocortex to the striatum in terms of a set of relatively segregated and specialized circuits or loops. These circuits largely preserve the functional topography of their cortical sites of origin, corresponding to oculomotor function, limbic function, sensorimotor function, etc. A major conceptual tenet of this "parallel organization" proposal was that each of the parallel circuits exhibited a form of integration such that functionally related cortical areas would project to overlapping zones in the striatum, thus providing a form of selective and specialized integration. At the same time, however, data suggested that different forms of cortico-striatal projection patterns, as well as subsequent striato-nigral projections, where further integration occurs, would provide for more complex integration that goes beyond the parallel circuit descriptions (Haber et al. 2006, 2000; Calzavera et al. 2007). In particular, it appears that information related to behavioral significance and reward has a special status and a special mode of projection or distribution in the cortico-striatal system (Haber et al. 2006). In this context it is now clearly established that the neurostransmitter dopamine (DA) which is a major component of the primate reward system plays a crucial role in cortico-striatal synaptic plasticity (Calebresi et al. 2007). One of the issues that we hope to address concerns how this plasticity may play a central role in language processing.

Over the last decades the cognitive neurosciences have provided vast data on the functional neurophysiology of language processing. This has allowed the emergence of models that synthesize these results into coherent frameworks. Friederici (2002) has proposed a detailed model of the temporal processing in sentence comprehension. Phase 1 involves

lexical categorization in superior and media temporal gyrus (STG and MTG) and the transfer of this information to the inferior frontal gyrus LIFG, and is associated with an early left anterior negativity in the 150-200 ms timeframe ELAN. In Phase 2 semantic and morphosyntactic integration take place in BA45/47 and BA44/45 respectively, associated with the N400 and left anterior negativity LAN respectively in the 300-500ms time frame. In Phase 3 a late syntactic integration takes place in IFG and BA44 and left frontal operculum and the basal ganglia (Friederici & Kotz 2003), associated with the P600. This phase is associated with reanalysis and repair processing. Such repair processing will require semantic working memory, which likely is provided by BA45/47 (Friederici 2002).

In a complimentary model, Hagoort has proposed a cortical continuum of integration/unification in his Memory, Unification and Control (MUC) model (2005), again paying particular attention to the link between function and neurophysiology. The mental lexicon, which allows retrieval of meaning based on lexical entries, is implemented in temporal cortex and retrieves for each word its meaning and its structural frame which specifies the possible structural environment of that lexical item. Unification requires a combination of distinct forms of working memory for integration in the time domain. In this context, semantic integration will thus imply BA 45/47, and syntactic integration imply BA 44/45.

We have recently proposed a model of grammatical construction processing in which grammatical structure cues (based on MacWhinney 1982) are encoded in a recurrent cortical network, and via corticostriatal associative memory retrieve the grammatical construction. This allows the mapping of semantic elements in BA45 onto the sentence level representation of meaning in BA44 (Dominey, Hoen, Inui 2006).

We have recently developed a neurophysiological model (Dominey & Inui, submitted) that begins to account for real-time aspects of sentence processing as specified in models

including those proposed by Friederici (2002), the functional processing of the memory, unification and control model of sentence processing developed by Hagoort (2005), and the grammatical construction processing model of Dominey, Hoen and Inui (2006). Part of the novelty of that research is that it also attempts to account for recent neurophysiological results concerning the processing of non-linguistic sequential material including artificial grammar learning (AGL) within the same framework. Above all, we want to situate this model in the context of distributed networks of cortical, basal ganglia and thalamic interaction, providing a more detailed link between processing and the underlying neurophysiology. An initial effort in this context has been made in Dominey and Inui (submitted). Here we expand on this approach and in particular address the implications of distinct corticostriatal circuits and their functional roles in language processing.

2. Corticostriatal Processing in Language

Figure 1 provides a functional neurophysiological overview of our proposal for corticostriatal function in language processing. In order to characterize the operation of this distributed network, we first specify the "goal" of the system in terms of sentence comprehension. Given an input sentence, the system should perform the necessary operations (e.g. lexical categorization, thematic role assignment etc.) in order to represent the meaning of the sentence. From a neurophysiological perspective, Tettamanti et al (2005) have demonstrated that listening to action-related sentences results in activation of frontoparietal motor circuits, including BA44, pars opercularis of the left inferior frontal gyrus (LIFG). For the present purposes, let us consider that during sentence comprehension LIFG BA44/6

recruits lexical information at the word level and unifies this into overall representations that span multi-word utterances (Hagoort 2005).

Here we consider the succession of events in time, within the space of the distributed brain network, for the processing of words in a sentence, leading to the generation of this sentence-level meaning representation in LIFG. In phase 1, a process of lexical categorization takes place as the word form is categorized. Based on Friederici (2002) this is hypothesized to take place in the temporal lobe with closed class information being processed in the STG, and open class information processed in the MTG.

Sakai (2005) reviews data indicating that BA45/47 is the putative area for selection and integration of semantic information at the sentence/discourse level. This suggests the possibility of a working memory for these elements that will allow their subsequent binding into the sentence level representation of meaning in BA44/6.

Information related to closed class words will be directed from STG to BA 47 in the IFG. In this context Inui et al. (2007) have observed that closed class elements in Japanese (particles) selectively activate BA47. Based on the layered structure of BA 47 we can also safely assume the existence of recurrent cortico-cortical connections within this area (Goldman-Rakic 1987). These provide an important context preserving/encoding capability (Dominey et al. 1995), so that BA47 activity represents the current closed class element within the overall context of the sentence. Continuing with the processing of closed class elements, we propose that corticostriatal projection neurons in BA47 project to the head of the caudate, in a canonical cortico-striato-nigro-thalamo-cortical circuit. Recent data from human cortico-striatal projection tracing using diffusion tensor imaging (Lehéricy et al. 2004) indeed support the proposal that corticostriatal connections in humans are organized in multiple overlapping circuits, similar to that observed in non-human primates (Alexander, Delong

Strick 1986). This leads us to propose a "grammatical structure" circuit in the cortico-striatal system with distinct and segregated paths, similar to the proposal of Ullman (2006).

We hypothesize that via this circuit, the system can retrieve information related to the syntactic roles (or frames in the unification component of the MUC model of Hagoort) that are licensed by this word or group of closed class words. One potential mechanism for establishing this encoding, that will take place during language acquisition, is via modifiable cortico-striatal synapses that form the basis for a robust form of associative memory. While the broad discussion of poverty of the stimulus etc. is beyond the scope of this paper (but see Dominey 2005a, b), let us consider that at some given point during early acquisition (18-24 months of age), the child hears a sentence and observes an action-scene which that sentence accurately describes. Further consider that the child is familiar with the words in the sentence, but not with the particular grammatical form, e.g. a passive of the form "John was introduced to Bill by Fred." Observation of the action will lead to a representation of that action in a structured manner (encoding who did what to whom) within the LIFG BA44 (see Tettamanti et al 2005).

When the sub-sequence "to Bill" is processed, and the system has the pre-established representation of Bill as the Recipient of the action, then conditions are favorable for learning the relation between "to" and assignment of the recipient role. The details of how this learning occur will be described in the next section. In summary, the encoding of the closed class word "to" in cortex and the recognition of the thematic role played by "Bill" generates activity in the caudate, which in turn inhibits SNr, disinhibiting thalamus and generating a final pattern of activation in BA 44/45M. We hypothesize that via this activation, the thematic role for the current open class "Bill" element is licensed to take the thematic role of recipient of the verb "introduced" (note that this is a language dependant operation – in other languages post-positions will license the word that precedes them). During learning, the

system will initially operate by trial and error. Successful trials in which the (initially random) choice of the system is correct will result in strengthening of the responsible cortico-striatal connections. Likewise, incorrect choices (resulting in incorrect thematic role assignments) will result in weakening of the responsible cortico-striatal synapses. This dual mechanism (strengthening and weakening appropriately) thus favor repetition and consolidation of correct responses, and elimination of incorrect responses. It should be made clear that the functional neurophysiology of this form of learning is quite well documented in the domain of sensorimotor sequence learning. If we consider that correctly understanding a sentence will generate some internal reward, then we can hypothesize that dopamine release in the striatum during correct trials in learning favors synaptic strengthening via LTP (Calabrisi et al 2007). Likewise the absence of this expected reward in the face of misunderstanding will lead to reduction in the baseline activity of dopamine producing cells in the SNc and VTA, and a corresponding weakening of these synapses (Calabrisi et al. 2007). The net result of this BA47/45 – Caudate – SNc – Thalamus – BA44/45 projection is a modulation of the licensing of the relevant open class element encoded in BA45 for its corresponding thematic role, which will be encoded in BA44. Thus, this cortico-striatal loop participates in the syntactic unification by establishing the licensed TRA. This is consistent with observations of increased activity in BA44 during tasks with high syntactic complexity (Stromswold 1991, Moro et al. 2001). In conditions in which the assignments cannot be made as each open class word arrives, the system will require a form of syntactic working memory. Fiebach et al. (2005) indeed observed activation of BA44 in conditions requiring such working memory. Given this "long loop" pathway, we will consider that this operation corresponds in part to the late Phase 3 integration of Friederici (2000) and Friederici & Kotz (2003).

Such a model would predict significant roles for striatum and thalamus in sentence processing. Indeed, this prediction is validated in a number of brain imagery and

neuropsychological studies. For example, Moro et al. (2001) observed significant activation of left BA45, and of the left caudate nucleus under conditions that specifically required syntactic processing. Similarly, during the processing of syntactic anomalies, Friederici & Kotz (2003) observed cortical activity in the left posterior frontal operculum adjacent to BA 44 and in the putamen of the left basal ganglia.

3.   From Neurophysiology to Neural Network Model

We can now proceed with the specification of the simulation model. The model architecture is illustrated in Figure 1. The cortical gradient of structural processing or unification is represented in the transition along BAs 47-45-44. Auditory or written word input undergoes an early lexical categorization, with closed class words making their way to BA47 via STG, and open class words to BA45 via MTG. BA45 encodes the current open class element, and a semantic working memory in BA45/47 maintains the sentence level ensemble of open class words available for possible reanalysis and repair. We model BA47 as a recurrent network which thus takes into account the current closed class element, as well as the previous closed class elements, with this history being encoded by information flow through the recurrent connections. BA47 projects to the head of the caudate, and via the "canonical" cortico – striato – nigro – thalamo – cortico circuit, projects to BA44/45M. While the current open class word is represented in BA45, the sentence level integrated meaning is represented in BA44/6 as proposed by Hagoort (2005). For simplicity, we assume a form of working memory with distinct neural populations corresponding to thematic roles, and distinct patterns of activity within those populations encoding the identity of the holder of that particular thematic role in the current sentence. This is represented in Figure 1 with the **P**redicate, **A**gent, **O**bject, **R**ecipient roles indicated by PAOR. The relation between these two representations is critical: As part of syntactic integration, the word level meaning (BA45)

must become integrated or bound – with the properly assigned thematic role – into the sentence level meaning in BA44/6. The assignment of a given open class element in a sentence to its thematic role will depend on multiple factors including the particular grammatical construction, the local and global configuration of closed class elements in the sentence, the relative order of the open class element in the sentence. The system must take these factors into consideration.

Given these requirements, and the neuroimaging evidence for activation of BA44/45 during syntactic processing, we can consider that there is a relatively complex interaction between BA44 and BA45. We thus propose two functional subdivisions of this region. BA44/45 M (for modulation) modulates the transfer or binding of semantic content in BA45 into the grammatical/thematic frame of meaning at the sentence level in BA44/6. Thus, the thalamocortical input will modulate the connections from BA45 to BA44/6 such that the open class element coded in BA45 is transmitted to BA44/6 appropriately in the context of thematic role assignment (as for "Bill" in Figure 1). The second functional subdivision, BA44/45 R (for recognition) plays a different role – recognizing the open class element in BA45 and its role in the meaning coded in BA44/6 (as for "Bill" in Figure 1). These two areas thus play reciprocal roles: during learning BA44/45R detects the thematic role binding for the current open class element, (e.g. recognizing that "Bill" in BA45 matches the Recipient (R) role in BA44/6), in the ongoing context of the sentence as encoded in BA47. BA44/45M provides the corresponding modulation or binding function, binding this element in BA45 to its proper role in BA44/6 during comprehension of the same type of sentence, when the same context is encoded in BA47. This recognition signal provides a crucial learning signal such that context encoding in BA47 becomes linked to the binding signal in BA44/45M (explained in the next paragraph). During comprehension, this activity in BA47 should drive the BA44/45M modulation population so that it modulates or binds the neural activity for the current open

class element onto its corresponding thematic role – the same thematic role that was recognized in BA44/45R during learning in the same context as encoded by BA47.

Let us reconsider the situation of learning a new grammatical structure mapping, in which case the system has observed an event and encoded that event in BA44/6. The system is now learning how to map the sequential succession of open class elements (in the corresponding sentence) onto their thematic roles. BA44/45 R (for recognition) compares the current open class element in BA45 ("Bill") with the event representation of BA44/6, and detects a match with the R (Recipient) role. This information projects via a corticostriatal pathway into the caudate nucleus in a zone that overlaps with the projections from BA47. The BA44/45R input provides a teaching signal specifying that the current activity in BA47 should drive binding of BA45 contents to the Recipient role. Through corticostriatal plasticity, corticostriatal synapses on striatal neurons that are activated by both the BA47 inputs the BA44/45R inputs will become strengthened in an associative memory that binds the BA47 and BA44/45R inputs together. The result of the learning is that at some future time, when the same sentence type is being processed, the same input from BA47 will activate the caudate –SNr-thalamus-BA44/45M pathway and retrieve the associated binding such that BA44/45M binds or modulates the current open class element into the Recipient role. Importantly, this learning will generalize to new sentences that adhere to the learned grammatical structure. Via this mechanism, corticostriatal plasticity is employed to allow closed class structure to drive thematic role assignment. Thus, the convergence of functionally related cortical projections onto the striatum provides a mechanism for learning how to perform thematic role assignment in real-time.

4.   Analysis of Language Dysfunction in the Context of the Model

The cortico-striatal system participates in language processing, and the details of this participation can be revealed in part through neurological studies. Thus, insults to the caudate via lesion (Alexander et al. 1987, Pickett et al. 1998), or Parkinson's and Huntington's disease result   in a broad spectrum of language deficits including deficits in syntactic comprehension (Grossman et al. 1999, Hochstadt et al. 2006, Teichmann et al. 2005) and grammatical rule processing (Ullman et al. 1997). Likewise, thalamic lesions can lead to linguistic deficits including deficits in sentence comprehension, and the use of syntactic complexity in production (De Witte et al. 2006).

More specifically, Hochstadt (et al. 2006) examined correlations between performance in syntactic comprehension and cognitive set-switching, verbal working memory, and articulatory rehearsal in a population of 41 Parkinson patients. They first observed a syntactic comprehension deficit for complex sentences in these patients. Interestingly, this impairment was correlated with the impairment in cognitive set-switching, in motor function (Hoehn-Yahr stage), and in reading span or verbal working memory. More detailed analysis suggested that deficits in set switching may be related to the processing of relative phrases, while deficits in working memory are related to impairments in comprehension of long-distance dependencies. The authors thus argue that such dissociated processes could reflect the dysfunction of distinct and segregated cortico-striatal circuits (Hochstadt et al. 2006).

Friederici and colleagues have taken a complimentary approach to investigating basal ganglia function in language processing through the use of analysis of brain activity in Parkinson's patients during syntactic processing (Friederici et al. 2003). These authors examined PD patients and age-matched controls in an auditory sentence comprehsneion task, and examine ERP responses related to early "first pass" syntactic processing (the ELAN), and to the later syntactic integration (the P600). Interestingly, PD patients did not differ from

controls with respect to the ELAN. However, their P600 response was different from that of controls as revealed by a significant group interaction effect.

In an attempt to synthesize these results, we can consider that for "canonical" sentences, first pass syntactic processing will provide the correct analysis. That is, the encoding of the current grammatical context in BA47 will activate, via direct corticocortical connections, the BA44/445M population which modulate the current open class element (coded in BA45) into its appropriate thematic role in the meaning representation in BA44/6. This corticocortical activation related to lexical categorization and early mapping processing involving STG, BA47 and BA44/6 will be responsible for the early ELAN ERP associated with first pass processing (see Friederici & Kotz 2003). Because these processes rely on cortico-cortical connections, and not on recruitment of the cortico-striatal system, they should remain relatively intact in Parkinson's disease. This is confirmed by the maintainence of the ELAN response in PD patients (Friederici & Kotz 2003), and by the maintained syntactic comprehension capability for canonical sentences (as in Hochstadt et al. 2006, Grossman 1999, Grossman et al. 2001). In cases of syntactic complexity or ambiguity in which first pass information is not sufficient – this will be recognized as a failure in the mapping process in BA44/6. In this case, the context encoding of sentence context in the recurrent BA47 network will activiate the striatum, and via cortico-striatal connections which have been modified through learning this activation will retrieve the correct mapping pattern which will be forwarded to the BA44/45M population via the SNR/GP-thalamo-cortical circuit as illustrated in Figure 1. In the case of a "reanalysis" in which erroneous thematic role assignments must be re-assigned, open class elements in the working memory of BA45/47 will be reassigned in parallel via activation of the BA44/45M population. This corresponds to the sentence level processing currently implemented in the model of grammatical construction processing of Dominey et al. (2006). This cortico-striato-cortical long loop activation will be associated

with the P600 and with these more complex syntactic processes. Thus, striatal dysfunction due to lesion or DA depletion will lead to corresponding impairments in this more complex syntactic processing.

5. Discussion

Over 20 years ago, Alexander, Delong and Strick (1986) presented ideas about the existence of segregated cortico-striatal pathways in which functionally related cortical regions would project to partially overlapping regions of striatum. Because this general structure is so recurrent we can consider that it is a fundamental aspect of primate brain organization. However, with respect to other fundamental organizational structures (e.g. topographic mapping, population coding) the computational power that is likely inherent in cortico-striatal segregated integration does not yet seem to be fully understood or exploited. Dominey et al. (1995) demonstrated how such integration could be exploited in learning to link visual color and shape inputs from inferotemporal cortex to oculomotor responses coded in the frontal eye fields via their common striatal target neuron (Dominey et al. 1995). The same cortico-striatal mechanism was demonstrated to generalize to allow the binding of internal state representations in recurrent prefrontal networks with the appropriate motor responses, again via their common striatal target neurons (Dominey et al. 1995). Recent data suggest that striatal neurons which receive inputs from BA46 are also inneravated by functionally related cortical areas which encode general representations of behavioural significance which will be well adapted for learning (Calzavara et al. 2007; Haber et al. 2006). Data from the investigation of the human corrticostriatal system allow us to extrapolate such results to man (Lehéricy et al. 2004). In particular, we propose the existence of a striatal region that receives converging inputs from two functionally related cortical areas in the left peri-sylvian region: BA 47 which encodes sentence grammatical context, and a population of neurons in BA44/45

which encode the relation between the current open class element during ongoing sentence processing, and its corresponding thematic role represented in the sentence-level representation of meaning in BA44/6. The central idea of our model is that via plasticity in corticostriatal synpases, this information about thematic role assignment in BA44/45M will become bound to the grammatical context coding activity in BA47, so that in the future the BA47 activity will be sufficient to retrieve the corresponding thematic role assignment information. Thus, the segregated convergence of language-related cortico-striatal projections provides the basis for syntactic comprehension.

Our proposal is thus that "overlearned" associations between grammatical structure representations and the corresponding thematic role assignments for canonical sentence types will be encoded and performed directly via cortico-cortical connections. In contrast, less frequent and more complex relations found in noncanonical sentences will rely on the corticostriatal system for a form of rule extraction (Ullman 1997, 2004, 2006, Teichman et al. 2005). Pasupathy and Miller have provided neurophysiological evidence that during the timecourse of learning arbitrary associations, the corticostriatal system will be involved in the early identification of the relevant associations. The output of basal ganglia will provide a mechanism by which slower cortico-cortical learning mechanism can subsequently acquire these associations. We can hypothesize such a mechanism here which allows the language learning system to adapt to the regularities of the target language, with high frequency canonical structures encoded in cortiococortical pathways and lower frequency non-canonical structures relying on the corticostriatal system.

The current model represents the next level of refinement of our efforts in understanding the brain mechanisms of syntactic comprehension and sentence processing. Dominey et al. (2003, 2006) began to lay the framework for syntactic comprehension and grammatical construction processing, and proposed that through corticostriatal plasticity, sentence level

coding of grammatical structure could become linked to the corresponding thematic role assignments. While these simulation studies demonstrated that the model could effectively learn a large ensemble of grammatical constructions in English, French and Japanese, there were two open issues. First, the neuranatomical details including the precise allocation of function to different cortical subdivisions was not yet available. Second, the ability of the model to perform on-line processing – as opposed to waiting until the end of the sentence before assigning thematic roles, was not clearly addressed. Recently, Dominey and Inui (submitted) proposed the next level of refinement in solutions to these two issues, based on the previous models, and current results from human brain imaging studies of language processing. In the current research, we continue this approach in order to develop a detailed proposition concerning cortico-striatal function in language processing, with an analysis of how the system will fail in response to dysfunction of the corticostriatal system. Our future research will include detailed validation of the model and analysis of its real-time processing capabilities. In the mean time, we hope that the current analysis will be of use in providing a common framework in which neuroimaging and neurological results can be considered within a common framework.

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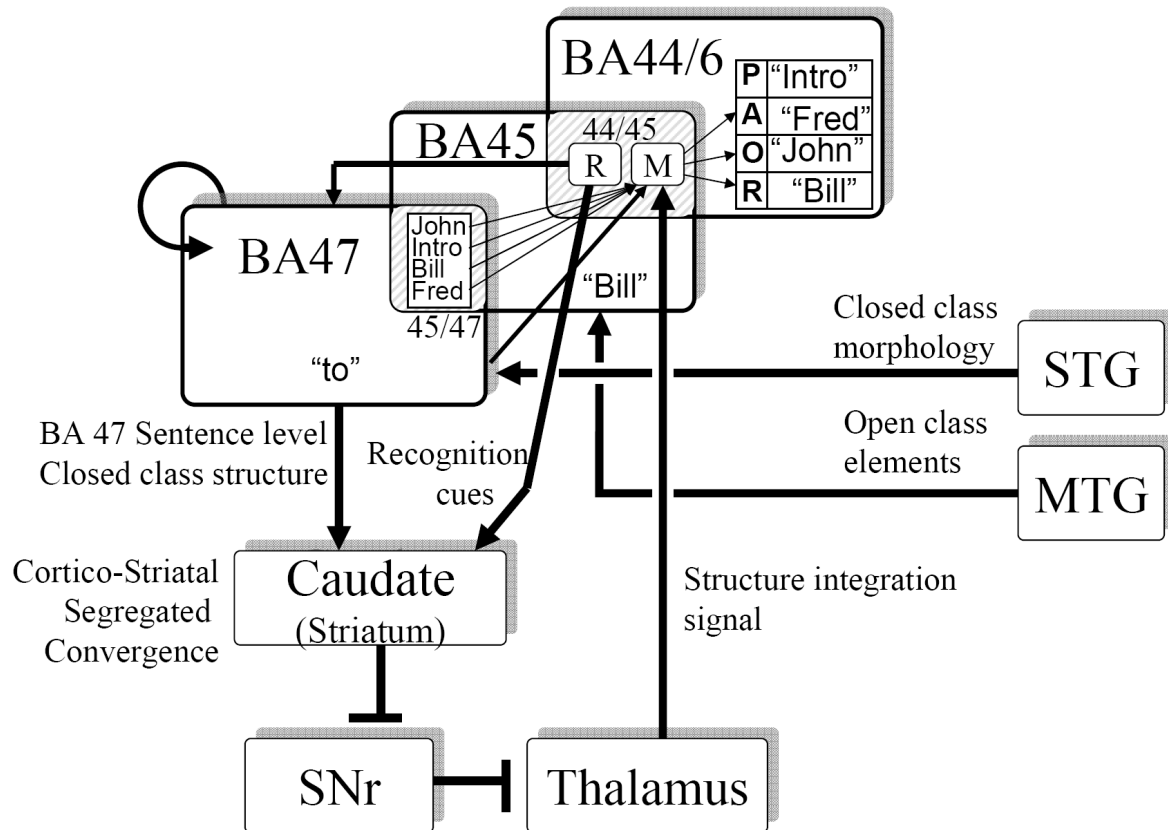
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Figure Captions:

Figure 1.   Syntactic comprehension model architecture.   Each of the labeled elements corresponds to a 5x5 array of leaky integrator neurons. Dual processing streams for closed and open class words, corresponding to STG and MTG respectively. As the input sentence is read in, the recurrent network BA47 encodes the ordered history of closed class words from STG. BA45 receives open class elements from MTG. BA44/6 serves as a syntactic working memory and the meaning in terms of a "predicate, agent, object, recipient" representation. Based on the syntactic context defined by the sequence of closed class words in the BA47 – Caudate projections, the thalamic inputs to BA44/45M will modulate the open class element from BA44 to the correct population in BA44/6. In BA44/6 "Bill" is represented in the Recipient population, corresponding to the correct mapping for an input sentence "John was introduced to Bill by Fred".

BA44/6

P	"Intro"
A	"Fred"
O	"John"
R	"Bill"

BA45

44/45 R M

John Intro Bill Fred

45/47

BA47

"to"

"Bill"

Closed class morphology

STG

Open class elements

MTG

BA 47 Sentence level Closed class structure

Recognition cues

Cortico-Striatal Segregated Convergence

Caudate (Striatum)

Structure integration signal

SNr

Thalamus

BA44/6/9 Integrated Working Memory representation of sentence meaning at multiword level. (P)redicate, (A)gent, (O)bject, (R)ecipient representation.

BA45 Semantic Working Memory for integration into BA44/6/9.

BA44/45R Recognize match between BA45 WM contents and an element of BA44/6

BA44/45M Map current semantic element (from BA45 for first pass, or BA45/47WM for 2nd)

BA45/47 Working Memory of input lexical semantic elements for possible late integration.

BA47 Recurrent network encoding sequential grammatical context

First Pass Mapping: BA47 to BA44/45M projection directs mapping of current semantic element onto appropriate role in sentence level meaning (BA44/6/9).

Late Integration: BA47 – Striatum … BA44/45M: By convergence of BA47 and BA44/45R, later BA47 activity drives striatal neurons linked with activation of appropriate BA44/45M neurons to perform late mapping of semantic element to its appropriate role.

Dominey Figure 1.