



Cortico-striatal language pathways dynamically adjust for syntactic complexity: A computational study



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ABSTRACT

A growing body of literature supports a key role of fronto-striatal circuits in language perception. It is now known that the striatum plays a role in engaging attentional resources and linguistic rule computation while also serving phonological short-term memory capabilities. The ventral semantic and the dorsal phonological stream dichotomy assumed for spoken language processing also seems to play a role in cortico-striatal perception. Based on recent studies that correlate deep Broca-striatal pathways with complex syntax performance, we used a previously developed computational model of frontal-striatal syntax circuits and hypothesized that different parallel language pathways may contribute to canonical and non-canonical sentence comprehension separately. We modified and further analyzed a thematic role assignment task and corresponding reservoir computing model of language circuits, as previously developed by Dominey and coworkers. We examined the models performance under various parameter regimes, by influencing how fast the presented language input decays and altering the temporal dynamics of activated word representations. This enabled us to quantify canonical and non-canonical sentence comprehension abilities. The modeling results suggest that separate cortico-cortical and cortico-striatal circuits may be recruited differently for processing syntactically more difficult and less complicated sentences. Alternatively, a single circuit would need to dynamically and adaptively adjust to syntactic complexity.

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1. Introduction

One of the most complex functions of the human brain is its capacity to communicate by language (Medaglia, Lynall, & Bassett, 2015). Exploring the neural basis of syntactic processing, i.e. the unique ability to combinatorially assemble words to form meaningful sentences, is one of the key challenges in cognitive neuroscience. It is generally accepted that syntactical operations are processed by a network of different cortical regions. The two main cortical regions with a central role in syntax are the inferior-posterior frontal cortex including Broca's area and the superior

temporal cortex (Friederici & Kotz, 2003; Grodzinsky & Santi, 2008; Pallier, Devauchelle, & Dehaene, 2011). However, subcortical grey matter structures also affect syntax and there is accumulating evidence that cortico-striatal pathways play a major role in syntactic language processing.

The striatum as the major input nucleus to the basal ganglia may impact language processing in several different ways (Dominey & Inui, 2009; Dominey, Inui, & Hoen, 2009). First, its role in non-language-specific functions such as *attentional resources* may have a general impact on language performances. Second, the striatum presumably subserves *phonological short-term memory capacities* which are necessary for accurate word perception in phrasal contexts. This latter role may contribute to morphological and syntactic rule application through maintaining intermediate language chunks such as morphemes and grammatical groups. Evidence exists that the basal ganglia chunks the representations

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of motor and cognitive action sequences (Destrebecqz et al., 2005; Kotz, Schwartz, & Schmidt-Kassow, 2009). Nigro-striatal circuits signal the initiation or termination of each action sequence, which occurs during sequence learning. Altering the function of the striatal circuit disrupts the development of start/stop activity and selectively impairs sequence learning (Badgaiyan, Fischman, & Alpert, 2007; Jin & Costa, 2010; Yin, 2010). It has been suggested that the striatum may also play a role in linguistic rule computation applying to particular kinds of morpho-syntactic rules (Teichmann, Darcy, Bachoud-Levi, & Dupoux, 2009).

Human cortico-striatal projection tracing with diffusion tensor imaging (Lehericy, Ducros, Krainik, et al., 2004) and anterograde tracing (Wiesendanger, Clarke, Kraftsik, & Tardif, 2004) showed that cortico-striatal connections in humans are organized in multiple overlapping circuits (Alexander, DeLong, & Strick, 1986). It was proposed that cortico-striatal projection neurons in Brodmann area 47 (BA 47) project to the head of the caudate, in a cortico-striato-nigro-thalamo-cortical circuit. The BA47 cortical region has a role in working memory for semantic features, thematic structure (Friederici, 2002), the unification of individual semantic features into an overall representation at the multi-word level (Turken & Dronkers, 2011). It seems that there exists a ‘grammatical structure’ circuit in the cortico-striatal system with distinct and segregated paths, similar to the proposal of Ullman (2001, 2006). Language disturbances related to cortico-striatal dysfunction are commonly encountered in a variety of neurological disorders. Patients with subcortical cerebrovascular damage, Parkinson’s disease and Huntington’s disease have difficulties suppressing semantically appropriate alternatives when trying to inflect novel verbs (Nemeth et al., 2012). This pathology may result from impaired function when the striatum is serving a non-language specific role in late inhibitory processing (Chan, Ryan, & Bever, 2011).

A recent study demonstrated that in patients with primary progressive aphasia, *syntactic processing* depends primarily on dorsal cortical and subcortical language tracts (Wilson et al., 2011). There was a strong correlation between reduced fractional anisotropy in the superior longitudinal fasciculus (including its arcuate component) and deficits in syntactic comprehension. It was suggested (Teichmann et al., 2009) that the ventral portions of the striatum may subserve linguistic rule computations, whereas more dorsally situated portions may underpin lexical operations (Teichmann & Gaura, 2008). Such sub-portions of the striatum are supposed to receive input from cortical areas which have been implicated in rule application and lexical processing (Broca’s area and posterior temporal cortices, respectively). So there is some evidence for a striatal “division of labor”, similar to what is seen in the cortical dual-stream model (Ueno, Saito, Rogers, & Lambon, 2011). The dorsal striatum’s role seems to be tied to motor responses (actor) versus the more cognitive-learning role (critic) of the ventral striatum. In the actor-critic architecture, the critic monitors and identifies patterns, such as motor contingencies, while the actor alters behaviors so as to improve the synchronization between environmental circumstances and behavioral responses (Reiss et al., 2005).

Recently, Dominey and colleagues presented a cortico-striatal reservoir computing model that reflects the recurrent fronto-cortical networks and where the output is represented by plastic cortico-striatal neurons. In this reservoir model, BA47 receives recurrent on-line input on word categories during sentence processing with plastic connections between striatum and cortex (Hinault & Dominey, 2013). The reservoir network consists of fixed connections encoding the spatiotemporal structure of an input sequence, while the connections to a readout layer are trained to produce a desired output in response to input sequences. It was shown that the recurrent reservoir successfully decodes grammatical structure from sentences in real-time. In the present study, we

have adapted this model to further study cortico-striatal function in sentence processing (Hinault & Dominey, 2013).

Sentence comprehension is based on the integration of associative and symbolic information (Townsend & Bever, 2001). More recently, it has been suggested that thematic role assignment for canonical and non-canonical sentence comprehension may require distinct spatio-temporal brain activity (del Rio et al., 2011). By using voxel-based lesion symptom mapping (VLSM) and fiber tracking in patients with fronto-striatal lesions, it was shown that perception of canonical sentences involved the BA44/45 areas and extended caudally to the underlying white matter, with no involvement of the deep white matter regions or the caudate (Teichmann et al., 2015). Non-canonical sentence perception, on the other hand, was associated with a region extending in BA44/BA45/BA47, throughout the intervening white matter, to the caudate head of the left striatum (Teichmann et al., 2015). The cortico-cortical pathways showed little overlap with the non-canonical syntax related VLSM clusters. These findings extend current syntax network models and correlate anatomically identified cortico-striatal pathways with complex syntax performance (Lehericy, Ducros, Krainik, et al., 2004; Lehericy, Ducros, Vd Moortele, et al., 2004; Teichmann et al., 2015).

In the present study, we elaborated on this concept by using a computational model of fronto-striatal syntax circuits (Hinault & Dominey, 2013). We hypothesized that comprehension abilities may differ between syntactically more simple and more complicated sentences and that the processing of sentences with different syntactic complexity may occur through contributions of separate cortico-striatal circuits. We examined the thematic role assignment ability of a reservoir network, where those model parameters were varied which influence the property of the network to retain information about the input for a certain time. Our study supports the observation that canonical and non-canonical sentence types requires different memory capacity for optimal processing. We propose that this might be via spatially distinct pathways (del Rio et al., 2011) or that the same network is capable of dynamically adjusting to the syntactic complexity. This second working hypothesis would be consistent with a more continuous, gradient-wise processing of syntactic complexity, with varying lengths of syntactic dependence.

2. Methods

2.1. Design

To illustrate the aim and the clinical implications of our computational study, we first present a selection of patient data from our recent publication (Teichmann et al., 2015). The rationale of that study was to explore whether the syntax network, in addition to the known cortico-cortical pathways, also involves a fronto-striatal pathway that accounts for the impact of the striatum on syntactic processing. The clinical test results of phrasal syntax task support the existence of a deep Broca-caudate pathway dedicated to particular aspects of syntax. We describe this here in detail (Teichmann et al., 2015).

2.2. Clinical case illustrations

Assessment of phrasal syntactic capacities was performed as part of our previous study (Teichmann et al., 2015). In summary, 12 patients were enrolled with lesions in the left frontal lobe and/or left striatum (Fig. 1 and Fig. 2) due to a WHO grade II glioma (Teichmann et al., 2015). Tumor resection was performed at least nine months prior to testing. Patients were right-handed, native French speakers and without previous history of neurological or psychiatric disease. In addition, 15 healthy controls matched with

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