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Role of the striatum in language: Syntactic and conceptual sequencing

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ABSTRACT

The basal ganglia (BG) have long been associated with cognitive control, and it is widely accepted that they also subserve an indirect, control role in language. Nevertheless, it cannot be completely ruled out that the BG may be involved in language in some domain-specific manner. The present study aimed to investigate one type of cognitive control—sequencing, a function that has long been connected with the BG—and to test whether the BG could be specifically implicated in language. Participants were required to rearrange materials sequentially based on linguistic (syntactic or conceptual) or non-linguistic (order switching) rules, or to repeat a previously ordered sequence as a control task. Functional magnetic resonance imaging (fMRI) data revealed a strongly active left-lateralized corticostriatal network, encompassing the anterior striatum, dorsolaterial and ventrolateral prefrontal cortex and presupplementary motor area, while the participants were sequencing materials using linguistic vs. non-linguistic rules. This functional network has an anatomical basis and is strikingly similar to the well-known associative loop implicated in sensorimotor sequence learning. We concluded that the anterior striatum has extended its original sequencing role and worked in concert with frontal cortical regions to subserve the function of linguistic sequencing in a domain-specific manner.

1. Introduction

Several lines of evidence have revealed that the basal ganglia (BG) are involved in language processing. Patients with stroke aphasia following focal BG damage often show a range of language impairments, including speech initiation problems, perseveration, reduced voice volume, foreign accent syndrome, lexical processing difficulty, and agrammatism (Alexander, Naeser, & Palumbo, 1987; Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 1994; Fabbro, 1999; Nadeau & Crosson, 1997; Wallesch & Papagno, 1988). Also, a bilingual patient's primary language can be more seriously disrupted than his/her second one (Fabbro, 1999, 2001). Neurological diseases affecting the BG and/or the related cortico-subcortical circuitry can also result in language disturbances. For example, Parkinson's disease patients sometimes show linguistic patterns similar to those typical of Broca's aphasia, including difficulty in producing regular past tense verbs (Lieberman et al., 1992; Ullman et al., 1997, see Longworth, Keenan, Barker, Marslen-Wilson, & Tyler, 2005 for a different view) and in comprehending complex syntactic constructions (Lieberman et al., 1992). Patients with Huntington's disease can also show sentence comprehension deficits (Teichmann et al., 2005), but their morphological problem is in sharp contrast to Parkinson's—they produce unsuppressed "-ed" suffixation (e.g. *walkeded*) instead of leaving out the suffix (Ullman et al., 1997, see Longworth et al., 2005 for a different view). Adolescents with Tourette's syndrome may demonstrate higher-order language processing difficulties, such as poor formulation of language output and/or reduced abstract/figurative language usage (Legg, Penn, Temlett, & Sonnenberg, 2005). A rare genetic disease involving mutations of FOXP2 can compromise the caudate nucleus and research has related this problem to an inability to repeat non-words with complex articulation patterns, which can result in a host of language impairments (Belton, Salmond, Watkins, Vargha-Khadem, & Gadian, 2003; Gopnik & Crago, 1991). Complementing neuropsychological findings, neuroimaging studies of healthy adults also suggested the implication of the BG, especially the striatum (caudate nucleus and putamen), in a wide variety of language tasks, including word generation (Crosson et al., 2003), semantic decisions about words which show language or meaning change from previous words (Crinion et al., 2006), ambiguity resolution of homonyms (Ketteler, Kastrau, Vohn, & Huber, 2008), sentence acceptability judgments (Moro et al., 2001), syntactic violations detection (Friederici, Ruschemeyer, Hahne, & Fiebach, 2003), syntactic ambiguity reading (Stowe, Paans, Wijers, & Zwarts, 2004), the application of implicitly learned rules in an artificial grammar task (Lieberman, Chang, Chiao,

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Bookheimer, & Knowlton, 2004), and the learning of artificial syntactic structures (Forkstam, Hagoort, Fernandez, Ingvar, & Petersson, 2006).

Although the involvement of the BG in language is repeatedly demonstrated in the literature, their precise role remains relatively unclear. To date, the dominant view holds that the BG do not play a direct role in language mainly because damage to these areas alone does not consistently produce classical aphasic symptoms (Crosson, 1992; Crosson, Benjamin, & Levy, 2007; Crosson & Haaland, 2003; Nadeau & Crosson, 1997) and because the language deficits induced by BG damage can usually be traced to cortical hypoperfusion (Hillis et al., 2002). Instead, the role of the BG may be in cognitive control, assisting language function by generally enhancing selected activities while suppressing competing ones (Crosson et al., 2003, 2007). Indeed, monolingual studies have corroborated that the BG are involved in the controlled process of syntactic integration (Friederici & Kotz, 2003; Friederici, Kotz, Werheid, Hein, & Yves von Cramon, 2003) and studies focusing on bilingualism have also shown that the BG are involved in second language comprehension and the control of switching between languages (Abutalebi, Miozzo, & Cappa, 2000; Abutalebi et al., 2008; Aglioti, Beltramello, Girardi, & Fabbro, 1996; Aglioti & Fabbro, 1993; Crinion et al., 2006; Friederici, 2006; Lehtonen et al., 2005; Price, Green, & von Studnitz, 1999). Even though it is generally agreed that the BG serve a domain-general control role, it cannot be completely ruled out that they might subserve some language-specific function. For instance, Robles, Gatignol, Capelle, Mitchell, and Duffau (2005) revealed a language-specific role associated with the dominant striatum using intraoperative electrical stimulations on 11 awake patients during brain surgery. Their paper reported that stimulation of the striatum in all the patients systematically elicited language disturbances, while no facial or limb motor effects were induced. The paper also found that stimulation of the caudate elicited perseveration while stimulation of the anterior putamen elicited dysarthria/anarthria. The authors suggested that this dissociation shows that the function of the caudate may be in selection/inhibition of language, while the anterior putamen may subserve the function of coordination of articulation.

To further understand if the cognitive control role of the BG is domain-general or can be language-specific, it is appropriate to focus on one particular control function and see if the BG implication differs between linguistic and non-linguistic dimensions. The particular function that our study aimed to investigate was sequencing—generation of an intended sequence through enhancing of desired elements while inhibiting undesired ones. Sequence learning has long been associated with the BG, especially in the acquisition and expression of sequences of behavior into meaningful, goal-directed repertoires in animals and humans (e.g. Graybiel, 1995; Squire & Zola, 1996). In language, the sequencing process appears at most linguistic levels, such as phonology—phonemes are joined in specific rule-based orders to form a word (e.g. "*help*", but not "*pleh*"), morphology—there are rule-based orders for adding inflectional (e.g. -s) and derivational (e.g. -ist) suffixes to a stem (e.g. "*natural-ist-s*", but not "*natural-s-ist*"), and, of course, syntax—information must be communicated in specific rule-bound orders (e.g. "*Reporters respect photographers*", but not "*Respect reporters photographers*"). Among the abundance of studies on the relationship between the BG and language, the investigations of dynamic aphasia (or transcortical motor aphasia) is particularly illuminating in the sequencing role of the BG in language. In line with the domain-general control role reviewed above (Crosson et al., 2003, 2007), research on dynamic aphasia revealed a sequencing function of the BG that was across different cognitive domains. For instance, Gold et al. (1997) argued that lesion to the circuit between dorsolateral prefrontal cortex and striatum could result in not only difficulties in executive functions but also a failure in forming concepts from within and developing a strategy to search the hierarchically organized semantic network. Pickett, Kuniholm, Protopapas, Friedman, and Lieberman (1998) also reported a dynamic aphasic patient with bilateral striatal damage, who presented with a cognitive set shifting deficit and problems with speech production and sentence comprehension. They attributed such deficits to a general poor control of cognitive sequencing. Robinson, Shallice, and Cipolotti (2006) and Crescentini, Lunardelli, Mussoni, Zadini, and Shallice (2008) studied dynamic aphasics and concluded that BG damage could result in impairment in generating a fluent sequence of novel thought in both verbal and non-verbal domains. Studies outside dynamic aphasia also have pointed to a domain-general sequencing role of the BG. For instance Longworth et al. (2005) examined a group of patients with subcortical cerebrovascular damage, Parkinson's disease and Huntington's disease and found that all these patients had difficulties suppressing semantically appropriate alternatives when trying to inflect novel verbs, which might result from striatum's serving a restricted, non-language specific role in late inhibitory process.

Recognizing the domain-general sequencing roles of the BG, some researchers went further and suggested an evolutionary link between linguistic and non-linguistic sequencing. Rodents have an innate syntax governing the serial order of grooming actions (Aldridge, Berridge, Herman, & Zimmer, 1993) and damage to their anterior dorsolateral neostriatum disrupts the serial order, but not the occurrence of the constituent movements of grooming (Cromwell & Berridge, 1996). Lieberman (2000), adopted an evolutionary approach and proposed that the grooming chain in rodents was analogous to syntax in human language. Dominey (1997) also argued that certain aspects of sequential cognition might contribute to human language processing, such as surface structure and thematic roles. He used a computational model to simulate circuits that mediate sensory-motor sequence learning in non-human primates (including cortical regions, BG, and thalamus), and found that this model not only reproduced complex spatiotemporal sequences, but also discriminated simple linguistic input. This demonstrates that the neural architecture that has evolved to support the sequential organization of movements may provide a basis for analogous functions in language.

The analogy from non-linguistic to linguistic sequencing is explicitly illustrated in Ullman's Declarative/Procedural Model (2004). Ullman proposed that, in the parallel and largely functionally segregated corticostriatal loops, similar computations may underlie sequencing in both non-linguistic (e.g. procedural learning) and linguistic (e.g. grammar) domains. According to Ullman, grammar is learned and processed by one or more of the corticostriatal loops, and such loop(s) may be domain-general (subserving grammar and other non-linguistic domains) or domain-specific (dedicated to grammar, and perhaps there are distinct (sub)loops for distinct grammatical sub-domains (e.g. syntax)). Ullman adds that although the grammatical (sub)loops might be domain-specific, they would still be part of a domain-general procedural system, in which the same or analogous computations were performed on parallel loops subserving various domains.

Even though most of the studies reviewed above point to an indirect/domain-general involvement of the BG in sequencing of language (e.g. Crescentini et al., 2008; Gold et al., 1997; Pickett et al., 1998; Robinson et al., 2006), the possibility that they might have some language-*specific* implication cannot be completely ruled out, as suggested by Robles et al.'s (2005) study with the intraoperative electrical stimulation technique. Of course, the evolutionary views held by Dominey (1997) and Lieberman (2000) connect linguistic sequencing with its potential precursor, but they do not preclude the possibility that the new sequencing function may have assumed a distinct/independent role in language. Also, Ullman (2004) has hypothesized that some corticostriatal loop(s) may