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

subserve language-specific sequencing function. Therefore, it would be interesting to find out if the BG, or more generally, any corticostriatal loop, have a language-specific sequencing role.

To address this, we created an experimental paradigm that directly contrasted linguistic and non-linguistic sequencing with normal healthy subjects undergoing functional magnetic resonance imaging (fMRI). The paradigm consisted of several tasks. One was a Linguistic Reordering task eliciting syntactic processing, in which the participants rearranged a short list of words/phrases into a sentence (e.g. RESPECT, REPORTERS, PHOTOGRAPHERS → "*Reporters respect photographers*" or "*Photographers respect reporters*"). An analogous Non-linguistic Reordering task required the participants to reorder the same list by shifting two starred items (e.g. *RESPECT, *REPORTERS, PHOTOGRAPHERS → "*Reporters respect photographers*"). We also added a set of tasks using conceptual materials to parallel syntactic tasks. The participants were instructed to reorder three taxonomically-related words along a "general-specific" dimension (e.g. TREE, PLANT, PINE → "*plant, tree, pine*"), or in the analogous Non-linguistic Reordering task, to switch the two starred items (e.g. *TREE, *PLANT, PINE → "*plant, tree, pine*"). The Linguistic and Non-linguistic Reordering tasks were carefully matched for experimental trials: they contained identical linguistic stimuli across subjects, and the output was always the same, either a grammatical sentence or a conceptual sequence. As a result, the major between-tasks difference was that one task required linguistic knowledge (syntactic or conceptual), while the other followed a simple Non-linguistic Reordering rule. Besides the two sequencing tasks, a baseline condition was added which required subjects to repeat a list of "correctly ordered" words/phrases. The output was also a sentence or a conceptual sequence. The use of repetition as the baseline task was to subtract out cognitive processes that were not the interest of current study, such as the preparation for performing a certain task when seeing the task instruction, word recognition and covert reading when subjects saw the visual stimuli, the comprehension process of the subjects when/if they realized that the output was a sentence or a conceptual sequence (in the Non-linguistic Reordering task) and motor planning for button press upon completing each trial. It is worth noting that, generally speaking, repetition itself was also a sequencing task—subjects still needed to sequence the presented stimuli one line after the other. However, it differed from the other two tasks in that there was no "active" sequencing on the subjects' part. Hence, the use of repetition as the baseline condition could subtract out many irrelevant processes shared by it and the other two reordering tasks, and thus give us activation maps mainly induced by the "sequencing" element that this study aimed to investigate. Finally, the participants were instructed to perform all the tasks in their head to avoid imaging interference from actual overt speech and to exclude brain response induced by speech production.

Our hypothesis was straightforward. Since BG were consistently involved in cognitive control in past research, we should observe BG activation in all three tasks: Linguistic Reordering,[1] Non-linguistic Reordering and Repeat. After subtracting out the activation of Repeat and focusing on the sequencing process, if the involvement of the BG was still domain-general, we should see similar activation patterns in Linguistic Sequencing (Linguistic Reordering vs. Repeat) and Non-linguistic Sequencing (Non-linguistic Reordering vs. Repeat); i.e., the activation would be equally strong if both reordering tasks induced stronger activation than Repeat, or absent, if both reordering tasks induced the same degree of activity as Repeat. On the other hand, if the BG had a sequencing role that was specific to language, activation should only be observed in Linguistic Sequencing (Linguistic Reorder-

ing vs. Repeat), but not in Non-linguistic Sequencing (Non-linguistic Reordering vs. Repeat).

2. Materials and methods

2.1. Subjects

Twenty-four neurologically healthy, right-handed subjects (18–31 years of age, mean age 24, 12 males) participated in this study after giving informed consent in accordance with the University of Arizona Institutional Review Board. Their right-handedness was determined by a simplified version of the Edinburgh handedness inventory (Oldfield, 1971). They were all native English speakers, and were all screened to rule out any history of neurological disorders that would interfere with language functioning. Each gender group was balanced for the presence of reported familial left handedness.

2.2. Materials

Seventy-two syntactic and 72 conceptual stimulus lists were constructed and counterbalanced across three experimental tasks—Linguistic Reordering, Non-linguistic Reordering and Repeat—such that each participant only saw each list once, and each list occurred equally often in the three tasks across participants. The required direction of reordering items to produce the correct output was closely matched across the Linguistic and Non-linguistic Reordering tasks. This was made possible by having an "expected response" for each trial (Table 1), derived from an independent prior behavioral pilot test by which the most frequent answer for each Linguistic Reordering trial was determined. This high probability response was treated as the expected answer and was used to decide which two items in the stimulus list were to be starred in the Non-linguistic Reordering task. For instance, for the list of "TREE, PLANT, PINE" in Linguistic Reordering, the expected conceptual sequence "*plant, tree, pine*" was produced by rearranging the first two items in the list. The same stimulus list was presented in the Non-linguistic Reordering task with the first two items starred, "*TREE, *PLANT, PINE", so that the same output would be produced when the list was reordered. For the Repeat task, the expected response was used. The same manipulation applied to the syntactic stimulus lists. Also, to make the syntactic reordering task as close to natural language production as possible, we carefully designed the materials so that subjects could only rely on the lexical information, but not the morphological information, to derive a sentence (see Table 1 for examples of materials and Supplementary Tables 1 and 2 for the complete lists of materials).

To prevent subjects from using their syntactic/conceptual knowledge to form the intended sequences all the time even

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[1] Throughout the article, when the names of tasks/contrasts/conditions are referred to, their first letters are capitalized (e.g. Linguistic Reordering, Linguistic Sequencing); otherwise, lower case letters are used (e.g. linguistic sequencing process).

Table 1
Examples of syntactic and conceptual materials. Despite the experimental task, the expected response is always a grammatical sentence for the syntactic materials and always a conceptual sequence for the conceptual materials.

Task	Sentence	Concept
Linguistic Reordering	RESPECT	TREE
	REPORTERS	PLANT
	PHOTOGRAPHERS	PINE
Non-linguistic Reordering	*RESPECT	*TREE
	*REPORTERS	*PLANT
	PHOTOGRAPHERS	PINE
Repeat	REPORTERS	PLANT
	RESPECT	TREE
	PHOTOGRAPHERS	PINE
Expected response	*Reporters respect photographers*	*Plant, tree, pine*

though the task instruction told them to do otherwise, 32 fillers (16 for each material type) that could not be formed into a sentence or a conceptual sequence were added to the experimental items. Also, to ensure that participants were paying attention, 4 of the 16 fillers for each material type were selected and combined with five new fillers, which could be reordered into a sentence or a general-specific sequence, to form a total of nine multiple-choice-question trials. In the end, there were a total of 72 experimental trials and 21 fillers, with nine of them followed by a multiple-choice question, for each material type.

2.3. Procedure

Prior to scanning, participants completed a practice session on a PC computer outside the scanner until reliable performance was demonstrated. They were then placed supine on the MRI table, fitted with VisuaStim digital goggles and two-way communication headphones (Resonance Technology Inc., Northridge, CA). During scanning, participants viewed the stimuli through the goggles, and a 3-button computer mouse was used to collect their behavioral responses. The computer presentation was controlled by DMDX Version 3.1.4.1 (Forster & Forster, 2003). Stimuli were presented vertically (to disrupt normal left-to-right reading processes) in uppercase yellow 12-pt Arial font, centered on a blue background.

The fMRI scan consisted of four sessions, two consecutive syntactic and two consecutive conceptual sessions, with the syntactic and conceptual sessions counterbalanced across subjects. Each trial began with a cue signaling the task that would follow. The cues for syntactic materials were "SENTENCE", "SWAP" and "REPEAT", and those for conceptual materials were "ORDER", "SWAP" and "REPEAT", for Linguistic Reordering, Non-linguistic Reordering and Repeat, respectively. On each trial, subjects first saw the task cue, displayed for 1.5 s, and then a stimulus list appeared on the screen. Subjects rearranged the list of words/phrases silently following the cue, and upon completing the task, pressed the left mouse button with their right index finger, which was recorded as reaction time (RT). The stimulus was then erased from the screen and was replaced by a cross (+) in the middle of the screen which remained visible for 4 s. Participants were instructed to fixate on the cross until the task cue for the next trial appeared. There was a 1 s inter-trial interval, for a total of 5 s between trials. Because the experiment was self-paced, the total time varied from trial to trial.

As mentioned in Section 2.2, nine filler trials for each material type (a total of 18 for the whole experiment) were added randomly where participants were required to answer a multiple-choice question after finishing a trial to ensure that subjects were attending to the tasks. On these trials, they reported what they just produced by picking one of three choices on the computer screen with a button press (first choice, left button; second choice, middle button; third choice, right button). The third choice was always "NONE OF THE ABOVE". After the button press, the screen returned to the usual "+" sign to signal the end of a trial (see Fig. 1 for an illustration of the procedure).

2.4. Image acquisition

Scanning was carried out on a 3T General Electric Signa scanner using an 8-channel phased array coil. Stimuli were presented on a computer equipped with custom hardware and a Measurement Computing PCI-DIO card to gather RTs and button press responses from the scanner. High-resolution T1-weighted images (direction = inferior to superior, matrix = 256×256, FOV = 24 cm, TE = 1.3 ms, TR = 625 ms, slices = 26, thickness = 5 mm, interscan spacing = interleaved) for the exact same slice selection as the following functional scans were first collected. Whole-brain functional images were then acquired in the anterior–posterior commissural plane using a single-shot spiral-in/out sequence (Glover & Law, 2001) (direction = inferior to superior, matrix = 64×64, FOV = 24 cm, flip angle = 90°, TE = 40 ms, TR = 2000 ms, slices = 26, thickness = 5 mm, interscan spacing = 0, voxel dimensions = 3.75 mm $\times$ 3.75 mm $\times$ 5 mm). Collection of functional imaging data began 12 s (6 TRs) after the start of the scan to allow magnetization to reach equilibrium. Four functional sessions were collected. For each session, a maximum of 260 volumes (approximately 9 min) were collected.

2.5. Image analysis

Data were preprocessed and analyzed using SPM5 (The Wellcome Department of Cognitive Neurology, London, UK) implemented in MATLAB 6.5.0 (The Mathworks Inc., Natick, MA). Each subject had four sessions of scanning: two consecutive syntactic and two consecutive conceptual ones. The two sessions with the same material type were pre-processed separately and then entered into one design matrix. Images were corrected for
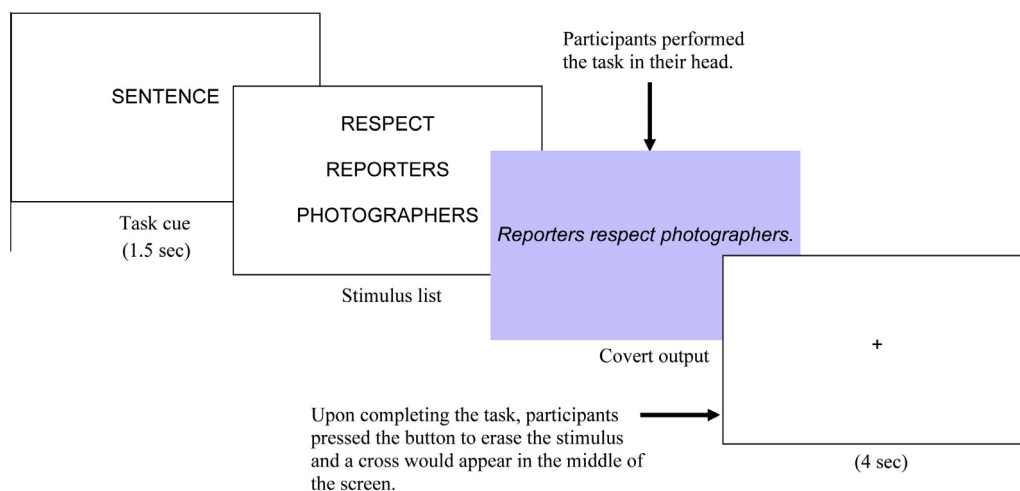

Fig. 1. Experimental procedure. On each trial, participants first saw the task instruction, which lasted for 1.5 s. Then a stimulus list appeared on the screen. The participants were required to rearrange the list of words/phrases in their head following the instruction. Upon completing the task, the participants pressed the left button of the mouse. The stimulus list was then erased from the screen and was replaced by a cross (+) in the middle of the screen which remained visible for 4 s. The participants were instructed to fixate on the cross until the instruction for the next trial appeared. For filler trials, instead of going to a cross directly, a multiple-choice question appeared and the participants were required to pick an answer that matched the output they just produced.

asynchronous slice acquisition using the middle anatomical slice as the reference slice, realigned to the first image for motion correction, normalized to the Montreal Neurological Institute (MNI) template, and smoothed using an 8-mm full-width half-maximum isotropic Gaussian kernel. After preprocessing, first-level fixed effects analyses were applied to each participant to estimate parameters for the different tasks with a general linear model. Serial correlations were estimated using an autoregressive AR(1) model during classical Restricted Maximum Likelihood (ReML) parameter estimation. Data were high-pass filtered using a cutoff of 128 s to remove slow signal drift. Regressors for each of the three tasks were defined, and additional regressors for task cue, filler trials, and the multiple-choice responses following the filler trials were included in the model as regressors of no interest. The hemodynamic response for each trial was modeled as an event starting with the appearance of the stimulus list and lasting 0 s using a canonical hemodynamic response function (HRF) without time and dispersion derivatives. T-contrasts were specified to test the experimental effects with the comparison of another condition or of the unmodelled, implicit baseline (i.e. the fixation on "+" which appeared for 4 s). For the group analysis, the output contrast images obtained from each participant were entered into second-level random effects analyses. These procedures provided whole brain activation maps thresholded at a false discovery rate (FDR) of 0.01 for the following contrasts for both material types presented in the Results section: (1) the main effects (compared with unmodelled implicit baseline), including Linguistic Reordering, Non-linguistic Reordering and Repeat, and (2) the sequencing conditions, including Linguistic Sequencing (Linguistic Reordering vs. Repeat), Non-linguistic Sequencing (Non-linguistic Reordering vs. Repeat) and Language-specific Sequencing (Linguistic Reordering vs. Non-linguistic Reordering). To visualize the overlap between Language-specific Sequencing for the syntactic and conceptual materials at the group level, the conjunction of the two activation maps was also calculated. This was done using the ImCalc feature in SPM5 by multiplying the two activation maps together. This procedure yielded a composite map containing only those voxels significantly activated at $P < 0.01$ (FDR-corrected) in each and both contrasts. The joint probability can be estimated by multiplying the probability for each contrast: $0.01 * 0.01 = P < 0.0001$ (FDR-corrected) (e.g. Cabeza, Dolcos, Graham, & Nyberg, 2002). The activation maps were visualized using the xjView toolbox (Version 8) (http://www.alivelearn.net/xjview).

3. Results

Both behavioral and functional imaging results are reported in this section. For the behavioral results, the analyses of variance (ANOVAs) were repeated measures, and an alpha value of 0.05 was adopted, with the Greenhouse–Geisser correction applied when appropriate. For follow-up paired *t*-tests, a two-tailed alpha level of 0.05 was chosen. For the imaging results, an alpha value of 0.01 (FDR-corrected) for the whole brain activation maps and a joint probability of $P < 0.0001$ (FDR-corrected) for the conjunction map were selected.

3.1. Behavioral data

Accuracy data were obtained from subjects' answers to 18 multiple-choice questions following filler trials. The accuracy rate was $91.2 \pm 7.7\%$ (mean ± SD), showing that participants were paying attention and understood the tasks. It is worth noting that the filler trials were originally included in the behavioral pilot test as experimental trials, but then excluded from the current imaging study because of their greater difficulty. Hence, the actual accuracy rate

for the experimental trials, which could not be directly assessed from subjects' covert response, was probably higher. In fact, we estimated the accuracy rate in our behavioral pilot test by asking our subjects to perform the syntactic and conceptual reordering tasks overtly (either by speaking their answers out loud or pushing buttons sequentially). Subjects' performance for the syntactic reordering task was almost perfect, and the accuracy rate for the conceptual reordering task was 97.1%.

RT was measured on each trial as the latency from the appearance of the stimulus to subjects' button press signaling their completion of the task. A 3 × 2 ANOVA with factors of Task (Linguistic Reordering, Non-linguistic Reordering, Repeat) and Material (Sentence, Concept) revealed a main effect of Task [$F(1.16, 26.60) = 140.46$, $P < 0.001$]. Follow-up *t*-tests indicated that RT was the longest for Linguistic Reordering, followed by Non-linguistic Reordering and then Repeat, for both the syntactic and conceptual material types [t's$(23) \geqslant 6.80$, P's < 0.001]. There was also a main effect for Material, showing that more time was needed for syntactic than for conceptual materials [$F(1, 23) = 4.70$, $P < 0.05$]. This was possibly due to higher cognitive load for syntactic materials because there were sometimes more words per syntactic trial [syntactic mean: 5.5; conceptual mean: 3]. The Material × Task interaction was also significant [$F(1.33, 30.69) = 18.55$, $P < 0.001$]. Follow-up tests indicated that while RTs were longer for the syntactic than for the conceptual materials in Non-linguistic Reordering and Repeat, [t's$(23) \geqslant 2.82$, P's < 0.05], this RT difference between material types disappeared in Linguistic Reordering [$t(23) = -1.42$, $P = 0.17$]. This may result from the difficulty of conceptual reordering: when asked which Linguistic Reordering task was more difficult after the experiment, 22 of the 24 subjects reported that reordering conceptual items was harder. This shows that although the cognitive load was generally heavier for syntactic than for conceptual materials (as demonstrated in the Material main effect), various Linguistic Reordering tasks could modulate the effect of cognitive load.

3.2. fMRI data

We performed whole-brain voxel-wise analysis on the imaging data, thresholded at $P < 0.01$ (FDR-corrected), to find out how the brain responded to various reordering tasks. Fig. 2 shows the statistical maps of the main effects of Linguistic Reordering, Non-linguistic Reordering and Repeat, compared with the umodelled, implicit baseline (i.e. the fixation on "+" which appeared for 4 s); Fig. 3, the conditions of Linguistic Sequencing (Linguistic Reordering vs. Repeat) and Non-linguistic Sequencing (Non-linguistic Reordering vs. Repeat); and Fig. 4, the Language-specific Sequencing condition (Linguistic Reordering vs. Non-linguistic Reordering).

As hypothesized, BG, along with many other cortical and subcortical brain regions, were strongly activated in both the Linguistic and Non-linguistic Reordering tasks (Fig. 2, left and middle columns). The BG were also activated in the Repeat task (Fig. 2, right column). The ubiquitous activation of the BG indicated that this brain region was indeed involved in cognitive control and also showed that our experiment tasks successfully recruited the BG.

We then compared the two reordering conditions with Repeat to examine the BG involvement in sequencing. First, in Linguistic Sequencing (Linguistic Reordering vs. Repeat), a left-lateralized frontal-subcortical network was strongly activated, including bilateral (left > right) inferior and middle frontal cortices (BA 44/45/47/46, especially Broca's area), dorsal medial frontal cortex (BA 8/9), premotor cortex, Supplementary motor area (SMA) and pre-supplementary motor area (pre-SMA, extending to anterior cingulate gyrus) and various subcortical structures, including the BG and part of the thalamus. Strong activation in the bilateral parieto-occipital lobe was also observed, including superior (BA 7) and inferior (BA 40) parietal lobules, precuneus (BA 7/19), cuneus (BA 19), lingual
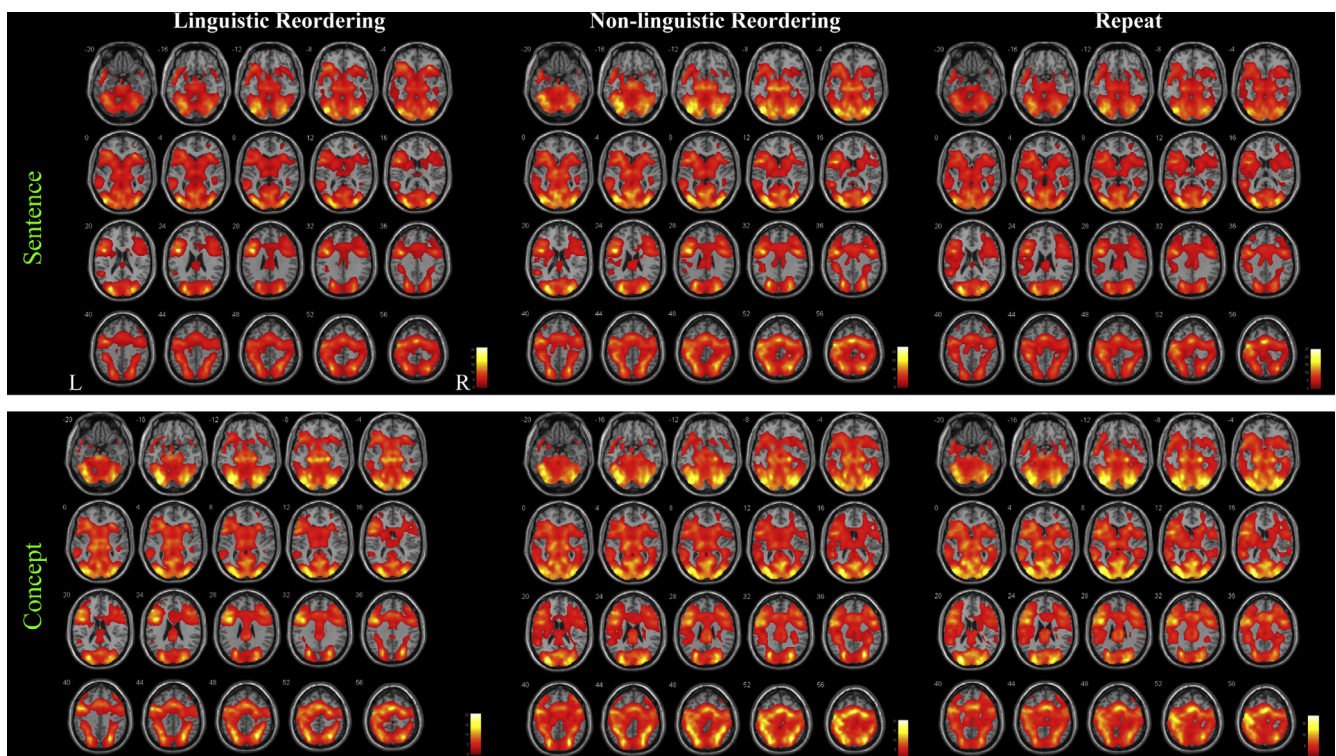
Fig. 2. Main effects of "Linguistic Reordering", "Non-linguistic Reordering" and "Repeat", compared with the umodelled, implicit baseline (i.e. the fixation on "+" which appeared for 4 s) at $P < 0.01$ (FDR-corrected), created by xjView using the single-subject brain in stereotactic space (MNI). Images are color coded, with hotter colors indicating stronger effects. Numbers are values on the Z axis. Upper, syntactic material; lower, conceptual material.
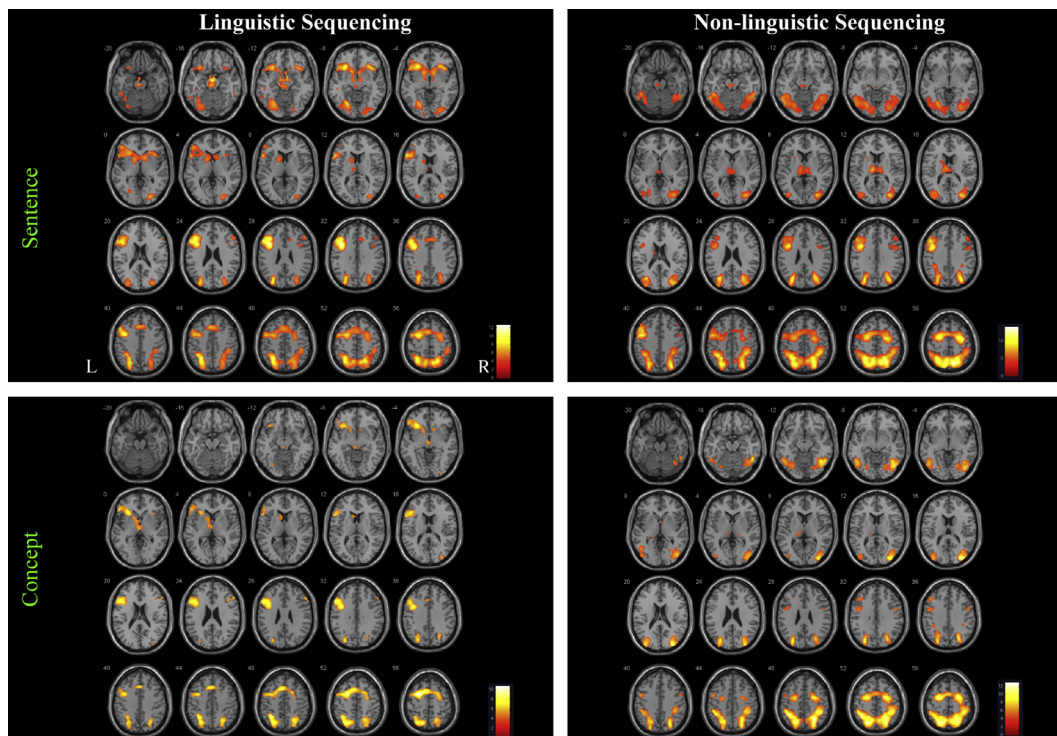

Fig. 3. Linguistic Sequencing (Linguistic Reordering vs. Repeat) and Non-linguistic Sequencing (Non-linguistic Reordering vs. Repeat) at $P < 0.01$ (FDR-corrected), created by xjView using the single-subject brain in stereotactic space (MNI). Images are color coded, with hotter colors indicating stronger effects. Numbers are values on the Z axis. Upper, syntactic material; lower, conceptual material.

gyrus (BA 18) and fusiform gyrus (BA 37). The overall activation pattern was similar across the two material types, with syntactic mate-

rials inducing additional activation in the left middle temporal (BA 20) gyrus and superior frontal gyrus.
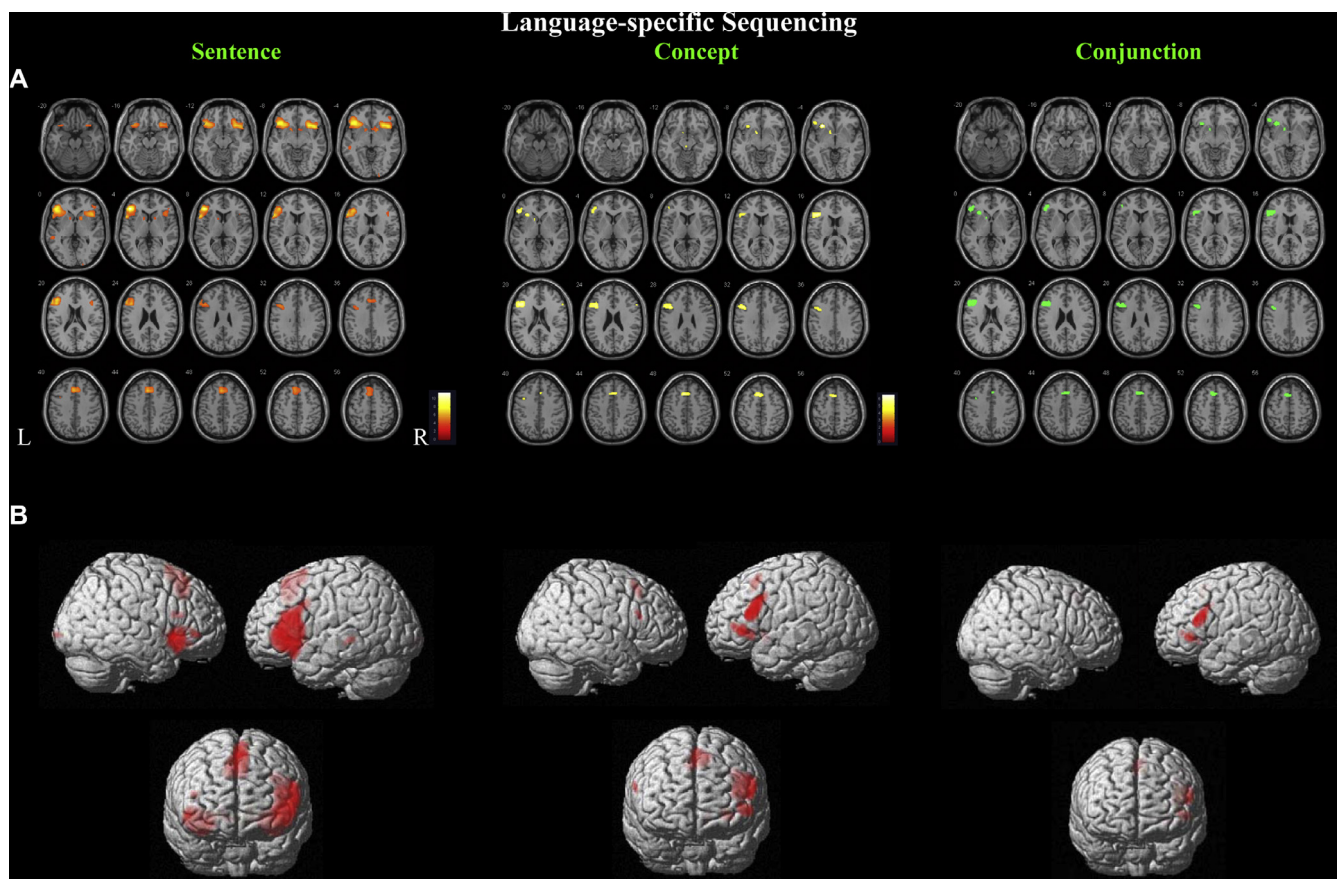
Fig. 4. Language-specific Sequencing (Linguistic Reordering vs. Non-linguistic Reordering) at *P* < 0.01 (FDR-corrected), created by xjView using the single-subject brain in stereotactic space (MNI). Slice views (A) and surface-rendered maximum-intensity projections (B) of the contrast with syntactic material (left), conceptual material (middle) and conjunction of the two (right). Images in (A) are color coded for syntactic (left) and conceptual (middle) materials, with hotter colors indicating stronger effects. Numbers are values on the *Z* axis.

In Non-linguistic Sequencing (Non-linguistic Reordering vs. Repeat), as in Linguistic Sequencing, there was strong activation in the left middle frontal gyrus, left medial frontal gyrus, and bilateral parieto-occipital lobe. However, along the left–right axis, whereas Linguistic Sequencing showed more left-lateralized cortical activation, the activation in Non-linguistic Sequencing was more symmetrical. More importantly, along the anterior–posterior axis, while Linguistic Sequencing demonstrated stronger anterior activation, including the inferior frontal lobe and the anterior striatum (Fig. 3, sentence: *z* = −20 to +16; concept: *z* = −12 to +24), Non-linguistic Sequencing failed to show such frontal-subcortical activation. Instead, it revealed more posterior activation in the parieto-occipital and temporo-occipital areas (Fig. 3, sentence: *z* = −20 to +16; concept: *z* = −20 to +24) and the thalamus (Fig. 3, sentence: *z* = +4 to +16; concept: *z* = +4 to +12).

To better capture regions that were more active in Linguistic than Non-linguistic Sequencing, we conducted an analysis of Language-specific Sequencing (Linguistic Reordering vs. Non-linguistic Reordering). Fig. 4 confirms our general impression on the difference between Linguistic Sequencing and Non-linguistic Sequencing that the activation for the former was more left-lateralized and more anterior. More importantly, the strongly activated frontal-subcortical circuit in Linguistic Sequencing survived the current comparison for both syntactic and conceptual materials albeit its size reduced in the latter—only inferior (extending to insula) and middle frontal gyri, pre-SMA (extending to anterior cingulate gyrus) and anterior striatum were activated. See Table 2 for the summary of the activated regions for Language-specific Sequencing.

To visualize the overlap of Language-specific Sequencing for syntactic and conceptual materials, we conjoined the two maps and showed their composite map in Fig. 4 (right column). The resulting conjunction map is almost identical to the activation map of Language-specific Sequencing for the conceptual materials, showing that the functional network of conceptual sequencing is almost fully embedded within that of syntactic sequencing. This suggested that these two types of language-specific sequencing processes might share the same underlying mechanism, but the more cognitively loaded syntactic materials recruited extra areas in the brain. See Table 3 for the summary of overlapping brain regions of Language-specific Sequencing for syntactic and conceptual materials.

In summary, our data revealed the implication of a frontal-subcortical network specifically in sequencing of language, encompassing the anterior striatum, the lateral prefrontal cortex (including DLPFC and VLPFC, which slightly extended to MFG and insula, respectively) and pre-SMA (slightly extending into the anterior cingulate gyrus).

4. Discussion

We created a reordering paradigm and asked subjects to perform tasks on language materials following implicit linguistic (syntactic and conceptual) or explicit non-linguistic (order switching) rules, with repeating the correct order as the control task. We aimed to discover whether the sequencing role of the BG in language was domain-specific. Our results showed that the BG, along with a widespread network of brain regions, were involved in both

Table 2
Summary of brain regions activated in Language-specific Sequencing (Linguistic Reordering vs. Non-linguistic Reordering) for syntactic and conceptual materials at $P < 0.01$ (FDR-corrected), with $x\ y\ z$ coordinates in MNI space. BA, approximate Brodmann's Area; MI, maximal intensity; L, left hemisphere; R, right hemisphere; IFG = inferior frontal gyrus; MFG = middle frontal gyrus; SFG = superior frontal gyrus, medFG = medial frontal gyrus; MTL = middle temporal lobe; DLPFC = dorsal lateral prefrontal cortex; VLPFC = ventral lateral prefrontal cortex.

Brain region		Extent (mm^3)	BA	MI (t)	x	y	z
Sentence							
IFG, insula, MFG, SFG	L	26,048	47/45/46/13/44	11.49	−44	36	6
	R	10,424	47/13/38/11/45	7.87	32	22	−8
medFG	L > R	9024	8/6/32/9	6.53	−2	26	42
MTL	L	488	21/22	4.94	−52	−34	−2
Cuneus	R	160	18	4.61	20	−104	−2
Anterior striatum (caudate head and putamen)	L	664		5.16	−12	10	−8
	R	1096		5.56	16	10	−4
Concept							
DLPFC, MFG	L	6360	9/45/46	6.14	−42	24	18
VLPFC	L	1448	47/45/46	5.96	−48	32	0
IFG	R	120	45/9/46	5.00	60	20	26
Insula	L	856	13/47	6.61	−30	26	−4
Pre-SMA	L > R	2496	8/32/6	6.01	−6	20	48
Anterior striatum (caudate head and putamen)	L	400		5.52	−10	8	−8

Table 3
Overlapping brain regions of Language-specific Sequencing (Linguistic Reordering vs. Non-linguistic Reordering) for syntactic and conceptual materials at the joint probability of $P < 0.0001$ (FDR-corrected) with $x\ y\ z$ coordinates in MNI space. BA, approximate Brodmann's Area; L, left hemisphere; R, right hemisphere; DLPFC = dorsal lateral prefrontal cortex; MFG = middle frontal gyrus; Pre-SMA = presupplementary motor area; VLPFC = ventral lateral prefrontal cortex.

Brain region		Extent (mm^3)	BA	x	y	z
DLPFC, MFG	L	5320	45/9/46	−50	20	12
VLPFC	L	1464	47/45	−44	30	−4
Insula	L	856	47/13	−28	22	−8
Pre-SMA	L > R	1984	8/32/6	6	22	40
Anterior striatum (caudate head and putamen)	L	224		−10	8	−10

the Linguistic and Non-linguistic Reordering tasks (Fig. 2). Performing the Repeat task (i.e. without "active" sequencing on the subjects' part) also recruited the BG (Fig. 2). This ubiquitous activation is in line with the widely-accepted view that the BG do not play a direct role in language, but serve a cognitive control function across different domains (Crosson et al., 2003, 2007). However, after subtracting the control condition (Repeat) from the two reordering tasks to isolate the sequencing component, the results revealed, among multiple activation foci in the brain, the involvement of a left-lateralized corticostriatal functional circuit in Linguistic Sequencing (Linguistic Reordering vs. Repeat), which included the anterior striatum, lateral prefrontal cortex (DLPFC and VLPFC) and pre-SMA. Although the Non-linguistic Reordering task in our study was somewhat "linguistic" due to the use of language materials, Non-linguistic Sequencing (Non-linguistic Reordering vs. Repeat) did not recruit this network; instead, its activation foci were more posterior and more symmetrical than those in Linguistic Sequencing. The fact that this corticostriatal circuit further survived the comparison of Linguistic Reordering vs. Non-linguistic Reordering (i.e. Language-specific Sequencing) confirmed that this network was significantly more sensitive to the linguistic sequencing process per se, not to domain-general sequence manipulation or to the use of language materials. In sum, our study clearly demonstrated that, by working in concert with cortical areas, the BG have extended their sequencing function to language in a domain-specific way.

How can the results support the domain-general role of the BG while revealing their language-specific involvement at the same time? The determination of a domain-general or -specific interpretation lies in the linguistic level that is targeted in a study. Take our experiment as an example. If we treated "the BG involvement of language" as their activation in a task that uses linguistic materials, then we would attribute an indirect role to the BG because they are activated in all three tasks. The omnipresent involvement of the BG

is not surprising because "cognitive control" exists in a wide variety of processes in all our tasks, such as word recognition, information retention in working memory, covert reading, decision making, just to name a few. On the other hand, when subtracting out irrelevant common cognitive components and focusing on the linguistic sequencing process, we clearly found the BG involvement in a language-specific manner. We should note the possibility that some language-specific activities of the BG might have existed in the brain map of the Linguistic Reordering task (Fig. 2), but the current fMRI technique did not have the kind of resolution to decipher them from Non-linguistic Reordering due to the well-acknowledged fact that the brain activation does not fully reflect different underlying neuronal activities (Logothetis, 2008). Future research using different kinds of techniques may shed some light on this issue.

We would like to emphasize again that the domain-general and -specific views can be reconciled in our study. As reviewed in the introduction, Ullman (2004) pointed out the possibility of having a domain-specific grammatical sub(loop) within a domain-general procedural system. The same possibility applies here: a language-specific loop for sequencing is embedded in a domain-general sequencing (or more generally, cognitive control) system. The basic computation for cognitive control in general, or sequencing in particular, may be similar across domains, but in processing linguistic materials, some language-sensitive component(s) may be added to the basic computation and thus a domain-specific process is created. The idea of "a domain-specific circuit within a domain-general system" may explain the inconsistent views about the sequencing role of the BG in previous literature. As mentioned in the introduction, past neuropsychological studies suggested a domain-general sequencing role of the BG (Gold et al., 1997; Pickett et al., 1998; Crescentini et al., 2008; Longworth et al., 2005; Robinson et al., 2006), while Robles et al.'s (2005) study using intraoperative electrical stimulation revealed a language-specific role of the

dominant striatum. Based on our "domain-specific within domain-general" interpretation, patients who showed deficits across different modalities might have larger damaged area, spanning over both language and non-language domains, while in a neurosurgery, the stimulated area could be more focal, and thus it is possible to probe into an area that is domain-specific.

Finally, to validate our interpretation that the BG involvement of linguistic sequencing is domain-specific, we need to rule out a few factors that have long been associated with BG activities: cognitive load, error correction and task switching. We first rule out the possibility of cognitive load. Our behavioral data showed that Linguistic Reordering took more time to complete than did Repeat (Linguistic Reordering > Repeat) and Non-linguistic Sequencing (Linguistic Reordering > Non-linguistic Reordering), which corresponded to the imaging data that the BG activity survived the comparisons of Linguistic Reordering vs. Repeat (i.e. Linguistic Sequencing) and Linguistic Reordering vs. Non-linguistic Reordering (i.e. Language-specific Sequencing), respectively. Nevertheless, our behavioral data also showed that subjects took more time to perform Non-linguistic Reordering than Repeat (Non-linguistic Reordering > Repeat), but the imaging data of Non-linguistic Reordering vs. Repeat (i.e. Non-linguistic Sequencing) did not demonstrate the implication of the BG. In fact, the BG activation pattern is in contrast to a component area of the discovered corticostriatal functional network, the DLPFC (BA 9 and 46). The DLPFC demonstrated a parallel between strong activation in the three contrasts (Linguistic Reordering vs. Non-linguistic Reordering, Linguistic Reordering vs. Repeat, Non-linguistic Reordering vs. Repeat) and the 3-step RT differences (Linguistic Reordering > Non-linguistic Reordering > Repeat). Previous literature has reported that the DLPFC is involved in tasks that require increased executive function (e.g. D'Esposito et al., 1995). Hence, this area may respond to the increased cognitive load in reordering tasks in a domain-general manner by providing the resources necessary for the sequencing process of language.

Another factor frequently associated with the BG is the error feedback processing (e.g. Lawrence, 2000). To demonstrate that the observed BG activity is unlikely due to the error feedback processing, we refer to the selection process of the experimental materials in the pilot test. Even though we asked our subjects to perform their tasks covertly in the scanner (to avoid unnecessary interference with signals) and thus could not estimate their accuracy rates for the reordering tasks specifically, our behavioral pilot test indicated that both the syntactic and conceptual reordering tasks were very easy for subjects. Although the pilot subjects also reported conceptual reordering being harder than syntactic reordering, as those subjects did in the fMRI experiment, their performance almost reached ceiling in both tasks. Therefore, the difficulty of the conceptual reordering task might have appeared as longer RTs but not with more errors in the behavioral data: although subjects usually spent less time in conceptual than syntactic trials due to the former having fewer words, their RTs did not differ between the conceptual and syntactic reordering tasks. Hence, even if subjects had made mistakes and then corrected themselves during the fMRI experiment, the problematic/noisy trials should have only made up a very small portion of the total trials. The final factor to rule out is the task switching factor. Each of our trials started with a task cue, so it is possible that such cues would introduce a task switching variable. However, the participants were always switching in performing the tasks (including Repeat), so this switching component was held constant and should be cancelled out in contrasts.

In addition to the language-specific role of the BG, the appearance of the sequencing network that the BG are embedded in is also an important finding of this study. This left-lateralized corticostriatal circuit has an anatomical basis. Diffusion tensor imaging (DTI) studies in humans (Lehéricy, Ducros, Krainik, et al., 2004; Lehéricy, Ducros, Van de Moortele, et al., 2004) have shown that the brain regions within this network are well-connected: the head of the caudate is connected to the VLPFC, DLPFC and pre-SMA, and the rostral putamen is also connected to similar cortical structures (although the caudate fibers were generally more rostral than those of the anterior putamen). Also, Duffau (2008) argued from DTI and intraoperative electrosimulation studies that a corticostriatal loop, connecting the fronto-mesial structures to the head of the caudate nucleus, was important in the control (i.e. selection, inhibition and programming) of language and in modulating a large distributed network of language in the brain, including a ventral semantic stream, a dorsal phonological stream, a speech perception pathway, and an articulatory loop. Furthermore, the anatomy of this corticostriatal circuit is strikingly similar to that of one of the parallel BG loops in primates and humans—the cognitive/associative/prefrontal loop (Alexander & Crutcher, 1990; Calzavara, Mailly, & Haber, 2007; Haber, Kim, Mailly, & Calzavara, 2006; Parent & Hazrati, 1995; Seger, 2009), which encompasses dorsolateral prefrontal, posterior parietal, head of the caudate and anterior putamen (Seger, 2006). This loop has been shown to be implicated in cognitive functions, such as sensorimotor sequence learning, attention, controlled retrieval and monitoring of information within working memory (Dominey, Hoen, Blanc, & Lelekov-Boissard, 2003; Grabli et al., 2004; Kostopoulos & Petrides, 2003; Levy & Goldman-Rakic, 2000; Petrides & Pandya, 2002). Hence, our findings indicate that the linguistic sequencing process may be recruiting a preexisting BG loop, instead of creating a new anatomical circuit de novo, which is in accordance with the principle of preadaptation that old structures can assume a new function during evolution (Bock, 1959; Gould, 1992). In this respect, our findings are in agreement with Dominey's (1997) argument that certain aspects of sequential cognition might contribute to human language processing and consistent with Lieberman's (2000) view of an evolutionary link between non-linguistic sequencing and syntax.

What roles may the component structures of this functional network play in linguistic sequencing? We already discussed the domain-general role of DLPFC previously, so we will focus on the other brain structures in this section. The linguistic sensitivity of this network may come from the close connection between the striatum and the VLPFC, including Broca's area (BA 45) and BA 47, which have been found to play important roles in a wide variety of language tasks (Friederici, 2002). It is generally accepted that one of the BG functions is the selection/control/gating of information generated in the cortex (e.g. Friederici & Kotz, 2003; Gurney, Prescott, Wickens, & Redgrave, 2004; Redgrave, Prescott, & Gurney, 1999); therefore, it is possible that through the neuronal connections between the anterior striatum and the VLPFC, the BG can modulate the linguistic sequencing process by inhibiting competition and enhancing the desired component (for details about the modulation, see Frank, 2006; for a similar mechanism of sequencing in motor movement, see Mink, 1996; for cognitive control in language, see Crosson et al., 2003 and Crosson et al., 2007). The involvement of the pre-SMA in linguistic sequencing is interesting but not surprising, as Crosson et al. (2003) also found pre-SMA as part of the functional circuit in lexical retrieval. In the motor domain, the pre-SMA has been shown to play an important role in determining (Rushworth, Walton, Kennerley, & Bannerman, 2004; Shima, Mushiake, Saito, & Tanji, 1996) and initiating (Cunnington et al., 2001; Kennerley, Sakai, & Rushworth, 2004; Lewis, Wing, Pope, Praamstra, & Miall, 2004) an action sequence in movement. Hence, the pre-SMA may play a similar role

in linguistic sequencing: determining a preferred sequence and initiating the sequencing process. Future work is needed to better understand the specific roles the component structures of the network may play.

Since sequencing is an essential component of language, the network discovered in this study should exert its power in various language processes. Even though our tasks are production ones, the network, at least part of it, may also be responsible for language comprehension. Dominey and Inui (2009) proposed a corticostriatal sentence comprehension model, and their modeled network is very similar to the functional network found in Linguistic Sequencing for syntactic materials (Fig. 3). It is possible that there is a common functional network responsible for the encoding and decoding of sequences in language, just as speech production and perception may share common neural substrates (Liberman & Mattingly, 1985). Future research addressing the decoding aspect of sequencing may shed some light on this view.

One might question that the tasks adopted in this study were not "natural" enough to proximate everyday language production and thus the emergent network might be task-dependent. However, when sequencing the syntactic materials, subjects needed to combine the lexical information generated by the stimulus list with their own syntactic knowledge to come up with a grammatical sentence (Levelt, 1999). They might also use their pragmatic knowledge to make sense of the final result, so that the re-ordered sequence was, for instance, "*The daughter upset the mother*" but not "*The mother upset the daughter*" (in our pilot test, the former was overwhelmingly more frequent than the latter, even though both were grammatical sentences). When sequencing the conceptual materials, subjects needed to probe into their lexicon, or more generally, the conceptual system of language, so that they could uncover the type relation in the stimulus list and produce correct general-to-specific sequences, such as "*plant, tree, and pine*". Since a speaker normally would not utter a list of nouns in a natural conversation, the conceptual sequencing task may seem less natural than the syntactic sequencing one. Nevertheless, the Linguistic Sequencing condition for the conceptual materials still presented a very similar activation pattern to that for the syntactic materials (Fig. 3). This suggests that the BG might be associated with some characteristic shared by syntactic and conceptual sequencing at a deeper level, which was not affected by the seeming "unnaturalness" of the conceptual reordering task. One educated guess about the shared characteristic may be the underlying hierarchical structure involved in reordering the materials. Decades of psycholinguistics research have revealed the psychological reality of syntactic hierarchical representation in language processing (see Townsend & Bever, 2001 for a review). Research has also reported the use of conceptual hierarchical structure in everyday language. Federmeier and Kutas (1999) conducted an event-related brain potential study to determine if a hierarchical semantic system was active in language comprehension. They found that subjects' processing was affected by hierarchical memory structure even though such structure was not needed to understand the sentence and was irrelevant to the experimental tasks. Also, Gold et al. (1997) demonstrated that damage to the circuit from the dorsolateral prefrontal cortex to the dorsolateral caudate led to problems with adequate activation of hierarchically organized semantic network, lending biological support for our speculation that the activation of the corticostriatal circuit in both material types may be due to the existence of hierarchical structure. Future research directly testing the relationship between the discovered functional network and the hierarchical structure in both linguistic (e.g. syntax, semantics, phonology) and non-linguistic (e.g. goal-directed actions) domains is needed to verify if the BG involvement is indeed language-specific, or if they are actually sensitive to domain-independent hierarchical structure.

In sum, our study clearly demonstrated that the BG work in conjunction with frontal cortical regions to subserve a language-specific role in sequencing. Future research is needed to explore other language-specific functions that the BG and this functional circuit might subserve, and to better understand the roles the component structures within the network may play in linguistic sequencing. Also, more work is in need to tease apart whether the BG involvement in linguistic sequencing is indeed domain-specific, or is actually sensitive to hierarchical structure across modalities.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.bandl.2011.11.005.

References

Abutalebi, J., Annoni, J.-M., Zimine, I., Pegna, A. J., Seghier, M. L., Lee-Jahnke, H., et al. (2008). Language control and lexical competition in bilinguals: An event-related fMRI study. *Cerebral Cortex, 18*(7), 1496–1505.

Abutalebi, J., Miozzo, A., & Cappa, S. F. (2000). Do subcortical structures control 'language selection' in polyglots? Evidence from pathological language mixing. *Neurocase, 6*(1), 51–56.

Aglioti, S., Beltramello, A., Girardi, F., & Fabbro, F. (1996). Neurolinguistic and follow-up study of an unusual pattern of recovery from bilingual subcortical aphasia. *Brain, 119*, 1551–1564.

Aglioti, S., & Fabbro, F. (1993). Paradoxical selective recovery in a bilingual aphasic following subcortical lesions. *Neuroreport, 4*(12), 1359–1362.

Aldridge, J. W., Berridge, K. C., Herman, M., & Zimmer, L. (1993). Neuronal coding of serial order: Syntax of grooming in the neostriatum. *Psychological Science, 4*, 391–395.

Alexander, G. E., & Crutcher, M. D. (1990). Functional architecture of basal ganglia circuits: Neural substrates of parallel processing. *Trends in Neurosciences, 13*(7), 266–271.

Alexander, M. P., Naeser, M. A., & Palumbo, C. L. (1987). Correlations of subcortical CT lesion sites and aphasia profiles. *Brain, 110*, 961–988.

Belton, E., Salmond, C. H., Watkins, K. E., Vargha-Khadem, F., & Gadian, D. G. (2003). Bilateral brain abnormalities associated with dominantly inherited verbal and orofacial dyspraxia. *Human Brain Mapping, 18*(3), 194–200.

Bock, W. J. (1959). Preadaptation and multiple evolutionary pathways. *Evolution, 13*(2), 194–211.

Cabeza, R., Dolcos, F., Graham, R., & Nyberg, L. (2002). Similarities and differences in the neural correlates of episodic memory retrieval and working memory. *NeuroImage, 16*(2), 317–330.

Calzavara, R., Mailly, P., & Haber, S. N. (2007). Relationship between the corticostriatal terminals from areas 9 and 46, and those from area 8A, dorsal and rostral premotor cortex and area 24c: An anatomical substrate for cognition to action. *European Journal of Neuroscience, 26*(7), 2005–2024.

Crescentini, C., Lunardelli, A., Mussoni, K., Zadini, A., & Shallice, T. (2008). A left basal ganglia case of dynamic aphasia or impairment of extra-language cognitive processes? *Neurocase, 14*(2), 184–203.

Crinion, J., Turner, R., Grogan, A., Hanakawa, T., Noppeney, U., Devlin, J. T., et al. (2006). Language control in the bilingual brain. *Science, 312*(5779), 1537–1540.

Cromwell, H. C., & Berridge, K. C. (1996). Implementation of action sequences by a neostriatal site: A lesion mapping study of grooming syntax. *The Journal of Neuroscience, 16*(10), 3444–3458.

Crosson, B. (1992). *Subcortical functions in language and memory*. New York: Guilford Press.

Crosson, B., Benefield, H., Cato, M. A., Sadek, J. R., Moore, A. B., Wierenga, C. E., et al. (2003). Left and right basal ganglia and frontal activity during language generation: Contributions to lexical, semantic, and phonological processes. *Journal of the International Neuropsychological Society, 9*(7), 1061–1077.

Crosson, B., Benjamin, M., & Levy, I. (2007). Role of the basal ganglia in language and semantics: Supporting cast. In J. Hart & M. A. Kraut (Eds.), *Neural basis of semantic memory* (pp. 219–243). Cambridge: Cambridge University Press.

Crosson, B., & Haaland, K. Y. (2003). Subcortical functions in cognition: Toward a consensus. *Journal of the International Neuropsychological Society, 9*, 1027–1030.

Cunnington, R., Egan, G. F., O'Sullivan, J. D., Hughes, A. J., Bradshaw, J. L., & Colebatch, J. G. (2001). Motor imagery in Parkinson's disease: A PET study. *Movement Disorders, 16*(5), 849–857.

D'Esposito, M., Detre, J. A., Alsop, D. C., Shin, R. K., Atlas, S., & Grossman, M. (1995). The neural basis of the central executive system of working memory. *Nature, 378*(6554), 279–281.

Dominey, P. F. (1997). An anatomically structured sensory-motor sequence learning system displays some general linguistic capacities. *Brain and Language, 59*(1), 50–75.

Dominey, P. F., Hoen, M., Blanc, J.-M., & Lelekov-Boissard, T. (2003). Neurological basis of language and sequential cognition: Evidence from simulation, aphasia, and ERP studies. *Brain and Language, 86*(2), 207–225.

Dominey, P. F., & Inui, T. (2009). Cortico-striatal function in sentence comprehension: Insights from neurophysiology and modeling. *Cortex, 45*(8), 1012–1018.

Dronkers, N. F., Wilkins, D. P., Van Valin, R. D. J., Redfern, B. B., & Jaeger, J. J. (1994). A reconsideration of the brain areas involved in the disruption of morphosyntactic comprehension. *Brain and Language, 47*(3), 461–463.

Duffau, H. (2008). The anatomo-functional connectivity of language revisited: New insights provided by electrostimulation and tractography. *Neuropsychologia, 46*(4), 927–934.

Fabbro, F. (1999). *The neurolinguistics of bilingualism*. East Sussex: Psychology Press.

Fabbro, F. (2001). The bilingual brain: Cerebral representation of languages. *Brain and Language, 79*(2), 211–222.

Federmeier, K., & Kutas, M. (1999). A rose by any other name: Long-term memory structure and sentence processing. *Journal of Memory and Language, 41*, 469–495.

Forkstam, C., Hagoort, P., Fernandez, G., Ingvar, M., & Petersson, K. M. (2006). Neural correlates of artificial syntactic structure classification. *NeuroImage, 32*(2), 956–967.

Forster, K. I., & Forster, J. C. (2003). DMDX: A windows display program with millisecond accuracy. *Behavior Research Methods, Instruments, Computers, 35*, 116–124.

Frank, M. J. (2006). Hold your horses: A dynamic computational role for the subthalamic nucleus in decision making. *Neural Networks, 19*(8), 1120–1136.

Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Sciences, 6*(2), 78–84.

Friederici, A. D. (2006). What's in control of language? *Nature Neuroscience, 9*(8), 991–992.

Friederici, A. D., & Kotz, S. A. (2003). The brain basis of syntactic processes: Functional imaging and lesion studies. *NeuroImage, 20*(Suppl. 1), S8–S17.

Friederici, A. D., Kotz, S. A., Werheid, K., Hein, G., & Yves von Cramon, D. (2003). Syntactic comprehension in Parkinson's disease: Investigating early automatic and late integrational processes using event-related brain potentials. *Neuropsychology, 17*(1), 133–142.

Friederici, A. D., Ruschemeyer, S.-A., Hahne, A., & Fiebach, C. J. (2003). The role of left inferior frontal and superior temporal cortex in sentence comprehension: Localizing syntactic and semantic processes. *Cerebral Cortex, 13*(2), 170–177.

Glover, G. H., & Law, C. S. (2001). Spiral-in/out BOLD fMRI for increased SNR and reduced susceptibility artifacts. *Magnetic Resonance in Medicine, 46*(3), 515–522.

Gold, M., Nadeau, S. E., Jacobs, D. H., Adair, J. C., Gonzalez Rothi, L. J., & Heilman, K. M. (1997). Adynamic aphasia: A transcortical motor aphasia with defective semantic strategy formation. *Brain and Language, 57*(3), 374–393.

Gopnik, M., & Crago, M. B. (1991). Familial aggregation of a developmental language disorder. *Cognition, 39*(1), 1–50.

Gould, S. J. (1992). Ontogeny and phylogeny – Revisited and reunited. *Bioessays, 14*(4), 275–279.

Grabli, D., McCairn, K., Hirsch, E. C., Agid, Y., Feger, J., Francois, C., et al. (2004). Behavioural disorders induced by external globus pallidus dysfunction in primates: I. Behavioural study. *Brain, 127*, 2039–2054.

Graybiel, A. M. (1995). Building action repertoires: Memory and learning functions of the basal ganglia. *Current Opinion in Neurobiology, 5*(6), 733–741.

Gurney, K., Prescott, T. J., Wickens, J. R., & Redgrave, P. (2004). Computational models of the basal ganglia: From robots to membranes. *Trends in Neurosciences, 27*(8), 453–459.

Haber, S. N., Kim, K. S., Mailly, P., & Calzavara, R. (2006). Reward-related cortical inputs define a large striatal region in primates that interface with associative cortical connections, providing a substrate for incentive-based learning. *Journal of Neuroscience, 26*(32), 8368–8376.

Hillis, A. E., Wityk, R. J., Barker, P. B., Beauchamp, N. J., Gailloud, P., Murphy, K., et al. (2002). Subcortical aphasia and neglect in acute stroke: The role of cortical hypoperfusion. *Brain, 125*, 1094–1104.

Kennerley, S. W., Sakai, K., & Rushworth, M. F. S. (2004). Organization of action sequences and the role of the pre-SMA. *Journal of Neurophysiology, 91*(2), 978–993.

Ketteler, D., Kastrau, F., Vohn, R., & Huber, W. (2008). The subcortical role of language processing. High level linguistic features such as ambiguity-resolution and the human brain; an fMRI study. *NeuroImage, 39*(4), 2002–2009.

Kostopoulos, P., & Petrides, M. (2003). The mid-ventrolateral prefrontal cortex: Insights into its role in memory retrieval. *European Journal of Neuroscience, 17*(7), 1489–1497.

Lawrence, A. D. (2000). Error correction and the basal ganglia: Similar computations for action, cognition and emotion? *Trends in Cognitive Sciences, 4*(10), 365–367.

Legg, C., Penn, C., Temlett, J., & Sonnenberg, B. (2005). Language skills of adolescents with Tourette syndrome. *Clinical Linguistics Phonetics, 19*(1), 15–33.

Lehéricy, S., Ducros, M., Krainik, A., Francois, C., Van de Moortele, P.-F., Ugurbil, K., et al. (2004). 3-D diffusion tensor axonal tracking shows distinct SMA and Pre-SMA projections to the human striatum. *Cerebral Cortex, 14*(12), 1302–1309.

Lehéricy, S., Ducros, M., Van de Moortele, P. F., Francois, C., Thivard, L., Poupon, C., et al. (2004). Diffusion tensor fiber tracking shows distinct corticostriatal circuits in humans. *Annals of Neurology, 55*(4), 522–529.

Lehtonen, M. H., Laine, M., Niemi, J., Thomsen, T., Vorobyev, V. A., & Hugdahl, K. (2005). Brain correlates of sentence translation in Finnish–Norwegian bilinguals. *Neuroreport, 16*(6), 607–610.

Levelt, W. J. M. (1999). Producing spoken language: A blueprint of the speaker. In C. M. Brown & P. Hagoort (Eds.), *The neurocognition of language* (pp. 83–122). New York: Oxford University Press.

Levy, R., & Goldman-Rakic, P. S. (2000). Segregation of working memory functions within the dorsolateral prefrontal cortex. *Experimental Brain Research, 133*(1), 23–32.

Lewis, P. A., Wing, A. M., Pope, P. A., Praamstra, P., & Miall, R. C. (2004). Brain activity correlates differentially with increasing temporal complexity of rhythms during initialisation, synchronisation, and continuation phases of paced finger tapping. *Neuropsychologia, 42*(10), 1301–1312.

Liberman, A. M., & Mattingly, I. G. (1985). The motor theory of speech-perception revised. *Cognition, 21*(1), 1–36.

Lieberman, P., Kako, E., Friedman, J., Tajchman, G., Feldman, L. S., & Jiminez, E. B. (1992). Speech production, syntax comprehension, and cognitive deficits in Parkinson's disease. *Brain and Language, 43*(2), 169–189.

Lieberman, M. D., Chang, G. Y., Chiao, J., Bookheimer, S. Y., & Knowlton, B. J. (2004). An event-related fMRI study of artificial grammar learning in a balanced chunk strength design. *Journal of Cognitive Neuroscience, 16*(3), 427–438.

Lieberman, P. (2000). *Human language and our reptilian brain: The subcortical bases of speech, syntax, and thought*. Cambridge: Harvard University Press.

Logothetis, N. K. (2008). What we can do and what we cannot do with fMRI. *Nature, 453*(7197), 869–878.

Longworth, C. E., Keenan, S. E., Barker, R. A., Marslen-Wilson, W. D., & Tyler, L. K. (2005). The basal ganglia and rule-governed language use: Evidence from vascular and degenerative conditions. *Brain, 128*(3), 584–596.

Mink, J. W. (1996). The basal ganglia: Focused selection and inhibition of competing motor programs. *Progress in Neurobiology, 50*(4), 381–425.

Moro, A., Tettamanti, M., Perani, D., Donati, C., Cappa, S. F., & Fazio, F. (2001). Syntax and the brain: Disentangling grammar by selective anomalies. *NeuroImage, 13*(1), 110–118.

Nadeau, S. E., & Crosson, B. (1997). Subcortical aphasia. *Brain and Language, 58*(3), 355–402.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*(1), 97–113.

Parent, A., & Hazrati, L. N. (1995). Functional anatomy of the basal ganglia. 1. The cortico-basal ganglia-thalamo-cortical loop. *Brain Research Reviews, 20*(1), 91–127.

Petrides, M., & Pandya, D. N. (2002). Comparative cytoarchitectonic analysis of the human and the macaque ventrolateral prefrontal cortex and corticocortical connection patterns in the monkey. *European Journal of Neuroscience, 16*(2), 291–310.

Pickett, E. R., Kuniholm, E., Protopapas, A., Friedman, J., & Lieberman, P. (1998). Selective speech motor, syntax and cognitive deficits associated with bilateral damage to the putamen and the head of the caudate nucleus: A case study. *Neuropsychologia, 36*(2), 173–188.

Price, C. J., Green, D. W., & von Studnitz, R. (1999). A functional imaging study of translation and language switching. *Brain, 122*, 2221–2235.

Redgrave, P., Prescott, T. J., & Gurney, K. (1999). The basal ganglia: A vertebrate solution to the selection problem? *Neuroscience, 89*(4), 1009–1023.

Robinson, G., Shallice, T., & Cipolotti, L. (2006). Dynamic aphasia in progressive supranuclear palsy: A deficit in generating a fluent sequence of novel thought. *Neuropsychologia, 44*(8), 1344–1360.

Robles, S. G., Gatignol, P., Capelle, L., Mitchell, M.-C., & Duffau, H. (2005). The role of dominant striatum in language: A study using intraoperative electrical stimulations. *Journal of Neurology, Neurosurgery, and Psychiatry, 76*(7), 940–946.

Rushworth, M. F. S., Walton, M. E., Kennerley, S. W., & Bannerman, D. M. (2004). Action sets and decisions in the medial frontal cortex. *Trends in Cognitive Sciences, 8*(9), 410–417.

Seger, C. A. (2006). The basal ganglia in human learning. *The Neuroscientist, 12*(4), 285–290.

Seger, C.A. (2009). The involvement of corticostriatal loops in learning across tasks, species, and methodologies In H. J. Groenewegen, P. Voorn, H. W. Berendse, A. B. Mulder, A. R. Cools (Eds.), *Basal ganglia IX: Proceedings of the international basal ganglia society* (pp. 25–39). Springer.

Shima, K., Mushiake, H., Saito, N., Tanji, J. (1996). Role for cells in the presupplementary motor area in updating motor plans. *Proceedings of the National Academy of Sciences, 93*(16), 8694–8698.

Squire, L. R., Zola, S. M. (1996). Structure and function of declarative and nondeclarative memory systems. *Proceedings of the National Academy of Sciences of the United States of America, 93*(24), 13515–13522.

Stowe, L. A., Paans, A. M. J., Wijers, A. A., & Zwarts, F. (2004). Activations of "motor" and other non-language structures during sentence comprehension. *Brain and Language, 89*(2), 290–299.

Teichmann, M., Dupoux, E., Kouider, S., Brugieres, P., Boisse, M.-F., Baudic, S., et al. (2005). The role of the striatum in rule application: The model of Huntington's disease at early stage. *Brain, 128*(5), 1155–1167.

Townsend, D., & Bever, T. G. (2001). *Sentence comprehension*. Cambridge: MIT Press.

Ullman, M. T. (2004). Contributions of memory circuits to language: The declarative/procedural model. *Cognition, 92*, 231–270.

Ullman, M. T., Corkin, S., Coppola, M., Hickok, G., Growdon, J. H., Koroshetz, W. J., et al. (1997). A neural dissociation within language: Evidence that the mental dictionary is part of declarative memory, and that grammatical rules are processed by the procedural system. *Journal of Cognitive Neuroscience, 9*(2), 266–276.

Wallesch, C.-W., & Papagno, C. (1988). Subcortical aphasia. In F. C. Rose, R. Whurr, & M. A. Wyke (Eds.), *Aphasia* (pp. 256–287). London: Whurr Publishers.