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The role of the striatum in linguistic selection: Evidence from Huntington's disease and computational modeling

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ABSTRACT

Though accumulating evidence indicates that the striatum is recruited during language processing, the specific function of this subcortical structure in language remains to be elucidated. To answer this question, we used Huntington's disease as a model of striatal lesion. We investigated the morphological deficit of 30 early Huntington's disease patients with a novel linguistic task that can be modeled within an explicit theory of linguistic computation. Behavioral results reflected an impairment in HD patients on the linguistic task. Computational model-based analysis compared the behavioral data to simulated data from two distinct lesion models, a selection deficit model and a grammatical deficit model. This analysis revealed that the impairment derives from an increased randomness in the process of selecting between grammatical alternatives, rather than from a disruption of grammatical knowledge *per se*. Voxel-based morphometry permitted to correlate this impairment to dorsal striatal degeneration. We thus show that the striatum holds a role in the selection of linguistic alternatives, just as in the selection of motor and cognitive programs.

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1. Introduction

Though research on the neural bases of language processing has mainly focused on cortical structures and their connections (Fedorenko, Behr, & Kanwisher, 2011; Friederici, 2012; Friederici & Gierhan, 2013; Hickok & Poeppel, 2007), subcortical structures and connections between cortical and subcortical systems are also part of the language network. The striatum is one of the most important subcortical structures involved in language processing. Evidence of striatal involvement in language was initially observed in neuropsychological studies of patients with focal striatal lesions (Cambier, Elghozi, & Strube, 1979; Cappa, Cavallotti, Guidotti, Papagno, & Vignolo, 1983; Damasio, Damasio, Rizzo, Varney, & Gersh, 1982; Demonet, 1997; Gronholm, Roll, Horne, Sundgren, & Lindgren, 2016; Nadeau & Crosson, 1997), and patients with neurodegenerative diseases causing striatal dysfunction, i.e., Huntington's and Parkinson's disease (Douaud et al., 2006; Stoessl, Lehericy, & Strafella, 2014). In a series of verb conjugation tasks Ullman and colleagues (Ullman, 2001, 2006; Ullman et al., 1997) found that English speaking Huntington's Disease (HD) patients over-regularize irregular verbs (e.g., **he runned* instead of *he ran*) and produced double-suffixations on regular verbs (e.g., *walk-ed-ed*). The authors interpret this deficit within a dichotomic model of language processing (Pinker, 1997), which consists of a 'mental lexicon' storing information, and a computational 'mental grammar' computing rules over stored abstract representations (Nemeth et al., 2012; Ullman, 2004, 2006; Ullman et al., 1997). Based on patients' deficits, the authors localize the neural correlates of the model's components, attributing lexical processing to the medial temporal lobe network, and grammatical processing to the fronto-striatal circuits. HD patients would thus be specifically impaired with the processing of linguistic rules. Teichmann and colleagues conducted similar experiments with French patients testing them on the production of future tense forms of non-existing (nonce) verbs (Teichmann et al., 2005, 2008). French has two regular patterns for the formation of the future tense: a frequent default pattern (first conjugation, e.g., *manger*–*mangera*) and a less frequent, non-default pattern (second and third conjugation, e.g., *dormir*–*dormira*), also called 'subregular'. In addition, like English, French also has a variety of highly restricted irregular alternatives (e.g., *venir*–*viendra*). The authors found that HD patients over-applied the most frequent rule to items belonging to the less frequent conjugation (e.g., *saurentir* –**saurentera*, instead of *saurentira*). The authors interpreted the results along Ullman's proposal. However, since the application of the default rule was spared in first conjugation verbs, they characterized the deficit in HD as being restricted to 'subregular' rules. In addition to this rule application deficit, De Diego-Balaguer and colleagues observed a rule-learning deficit in a comparable sample of early French HD patients tested on the learning of a simplified artificial language in which words and rules could be extracted (De Diego-Balaguer et al., 2008). The authors also report results from pre-manifest carriers of the HD mutation, whose performance was not quantitatively different from the one of matched controls in the learning task, but who showed a qualitative difference in the level of abstractedness of the acquired rule.

Within the neuropsychological literature, other experimental results suggest that, rather than being recruited for rule learning and rule application, the striatum is needed at late processing stages requiring selection and inhibition between competing alternatives (Copland et al., 2003; Garcia et al., 2017; Longworth, Keenan, Barker, Marslen-Wilson, & Tyler, 2005; Sambin et al., 2012) and syntactic reanalysis (Kotz, Frisch, von Cramon, & Friederici, 2003). Neuroimaging studies of healthy subjects also provide data compatible with this alternative proposal. The left dorsal striatum in particular is activated in tasks requiring reanalysis of ambiguous or incorrect sentences (Friederici & Kotz, 2003; Mestres-Misse, Turner, & Friederici, 2012; Moro et al., 2001; Tettamanti et al., 2005). A role of the striatum in linguistic tasks requiring cognitive control also emerges from studies of bilingual speakers (Abutalebi et al., 2013; Crinion et al., 2006; Friederici, 2006).

In sum, despite the wide variety of data showing an involvement of the striatum in language processing, its specific role remains unclear. Ullman's proposal that the striatum is recruited for the computation of grammatical rules is challenged by French HD data, showing rather that only certain rules are affected by striatal atrophy, and by the large body of data showing that the striatum is implicated in syntactic reanalysis and in the inhibition of competing alternatives. Moreover, the dichotomist distinction between regular and irregular morphological processes underlying Ullman's and Teichmann's proposals has been questioned in the morphological literature by proposals of unified systems subsuming both processes (Albright & Hayes, 2003; Meunier & Marslen-Wilson, 2004; Plunkett & Marchman, 1993; Rumelhart & McClelland, 1986).

In this paper we propose that in order to identify the specific role of the striatum in language processing it is necessary to consider an alternative to the proposals sketched above. More precisely, it is necessary to consider that the striatum plays a more general role in linguistic processing, akin to the role it plays in other cognitive domains, such as motor control, attention, planning and decision-making (Alexander, DeLong, & Strick, 1986; O'Doherty et al., 2004). Results obtained from neurophysiology and neuroimaging suggest that this structure filters cortical information to drive decision-making. Specifically, the striatum, and particularly its dorsal parts (caudate nucleus and putamen), plays a key role in the 'action selection' process (Kable & Glimcher, 2009; Montague & Berns, 2002; Rangel, Camerer, & Montague, 2008), by weighting the values assigned to the different options made available by the prefrontal cortex (Hare, O'Doherty, Camerer, Schultz, & Rangel, 2008; Padoa-Schioppa & Assad, 2008).

In the domain of linguistic theory, this decomposition of the decision process into value assignment and selection exhibits strong analogies with the processes assumed within the framework of Optimality Theory (OT) (Prince & Smolensky, 1993/2004). OT divides speech production into two components. The evaluation component assigns wellformedness values to possible spoken outputs given an underlying lexical input. The selection component selects the optimal output on the basis of these values, like action selection. According to OT, optimization is a general organizing principle underlying neural computation that can be adapted to the theory of

language. Whereas evaluation is dependent on language-specific grammatical constraints, the operations of the selection component can be viewed as domain-general, analogous to those involved in non-linguistic selection.

Here, we use OT as it provides us with the framework allowing us to assess whether the role of the striatum in linguistic processing is analogous to its role outside of language. Specifically, we hypothesize that the striatum is recruited for the selection of linguistic alternatives, as for the selection of motor and other programs. To test this hypothesis we studied patients with HD, as this inherited neurodegenerative disease is a good model of striatal lesion in its early stages (Douaud et al., 2006; Tabrizi et al., 2009; Vonsattel et al., 1985). We independently validated our HD population as an appropriate model of patients with striatal lesions, by comparing structural brain atrophy in these patients to a population of healthy matched controls, by voxel-based morphometry (VBM).

The linguistic tasks previously used to reveal a role of the striatum in language processing do not allow us to test our hypothesis. Tasks involving verbal conjugation in English and French (e.g., Today he walks, yesterday he … *walked*) (Teichmann et al., 2005, 2008; Ullman et al., 1997) are not suited to test the selection process, as a limited number of alternatives is available (i.e., English past tense: regular *vs* irregular; French future tense: regular, 'subregular', irregular). In addition to being very few in number, the alternatives within the set are not comparable with each other as some are regular alternations undergone by a large set of lexical items and others are irregular, i.e., lexically very restricted. Tasks involving syntactic reanalysis or lexical inhibition are in principle better suited to test linguistic selection processes. However, these tasks are not standardly modeled within OT and thus the relative contribution of the selection and the evaluation component is hard to assess.

We therefore set out to design a new task which could be modeled within OT, and in which several comparable linguistic alternatives must be evaluated before selection. To assess whether the striatum holds a role in evaluation or in selection processes, we compared the performance of HD patients in this task with that of matched controls.

The grammar of French adjectives is the ideal paradigm to test linguistic selection. Unlike in English, where gender differences are not pronounced [compare small-FEMININE (FEM) and small-MASCULINE (MASC)], in French adjectives take on different forms depending on their gender (compare *sportive*-FEM and *sportif*-MASC 'athletic'). There are four common patterns of alternation, Fig. 1a. These patterns are regular and instantiated by a large number of items in the French lexicon. This allows investigating the role of the striatum in evaluation and selection without the confounding distinction between regular, subregular and irregular morphological processes. We designed an elicitation task, in which participants were given the feminine form of a nonce adjective, and had to produce the corresponding masculine. The feminine form was provided, as it is the underlying form of the adjective, i.e., the form from which the masculine is derived.

The task requires grammatical knowledge about the four patterns and about their respective wellformedness values in different linguistic contexts (evaluation). It also requires selecting among these patterns, to produce the one with the highest value (selection).

If the evaluation process is impaired, patient should produce responses incompatible with the underlying grammar of control participants. More specifically, patients' responses should be the output of a grammar in which constraints are ranked differently than those in the grammar of controls, and thus evaluated differently. By contrast, if the selection process is impaired, patients should produce a response pattern very similar to that of controls – i.e., evaluated by the same language-specific constraint ranking, but with increased randomness and a more frequent selection of non-optimal alternatives.

To determine the specific function of the striatum in language, we instantiated computational models of both evaluation and selection deficits using OT. We modeled the French adjective system within Maximum Entropy Harmonic Grammar [MaxEntHG (Goldwater & Johnson, 2003; Hayes & Wilson, 2008)], a probabilistic variant of OT, and trained our model on the data from our population of healthy controls. The computational model was then 'impaired' in two ways to test our hypothesis. One impairment model simulated a grammatical deficit, introducing noise in the constraint-based evaluation process (Goldrick & Daland, 2009). The other model simulated a selection deficit by increasing randomness in the selection process (Palminteri et al., 2012), i.e., by selectively attenuating the signaling of the possible outcomes. Computational modeling allows to refine our hypotheses and to directly test their predictions. If patients' impairment is in the evaluation process, we expect the model simulating a grammatical deficit to provide a better fit to the data produced by the patients. On the contrary, if their impairment is in the selection process, we expect the model simulating a selection deficit to provide a better fit to their data.

Additionally, we used VBM to assess whether the linguistic deficit in HD patients was correlated with striatal atrophy.

2. Material and methods

2.1. Participants

We included thirty carriers of the mutation responsible for HD (abnormal CAG expansion in the Huntingtin gene) and thirty healthy controls with no family history of HD and no neurological or psychiatric disorder. Patients were in the early phase of the disease, stage I of the classification based on the Unified Huntington Disease Rating Scale [UHDRS (Huntington Study Group, 1996)] total functional capacity (TFC) scale. Control participants were matched to patients for age [$t_{55} = -.01$, $p = .99$; Cohen's $d = -.003$, C.I. (−.52, .51)], sex [$\chi^2(1) = 0$, $p = 1$; OR = .87, C.I. (−.7, .88)], handedness [$\chi^2(1) = .88$, $p = .35$; OR = .8, C.I. (−.8, 1.1)] and educational level [$t_{57} = .83$, $p = .41$; Cohen's $d = .22$, C.I. (−.3, .73)]. Twenty-five HD patients were able to undergo a structural MRI scan within a three-month window around the linguistic task. Brain atrophy in patients was assessed by comparing their MRI scans with those of twenty-five additional healthy control subjects matched for age and sex. Information about handedness and educational level was not available for this group of control subjects. This

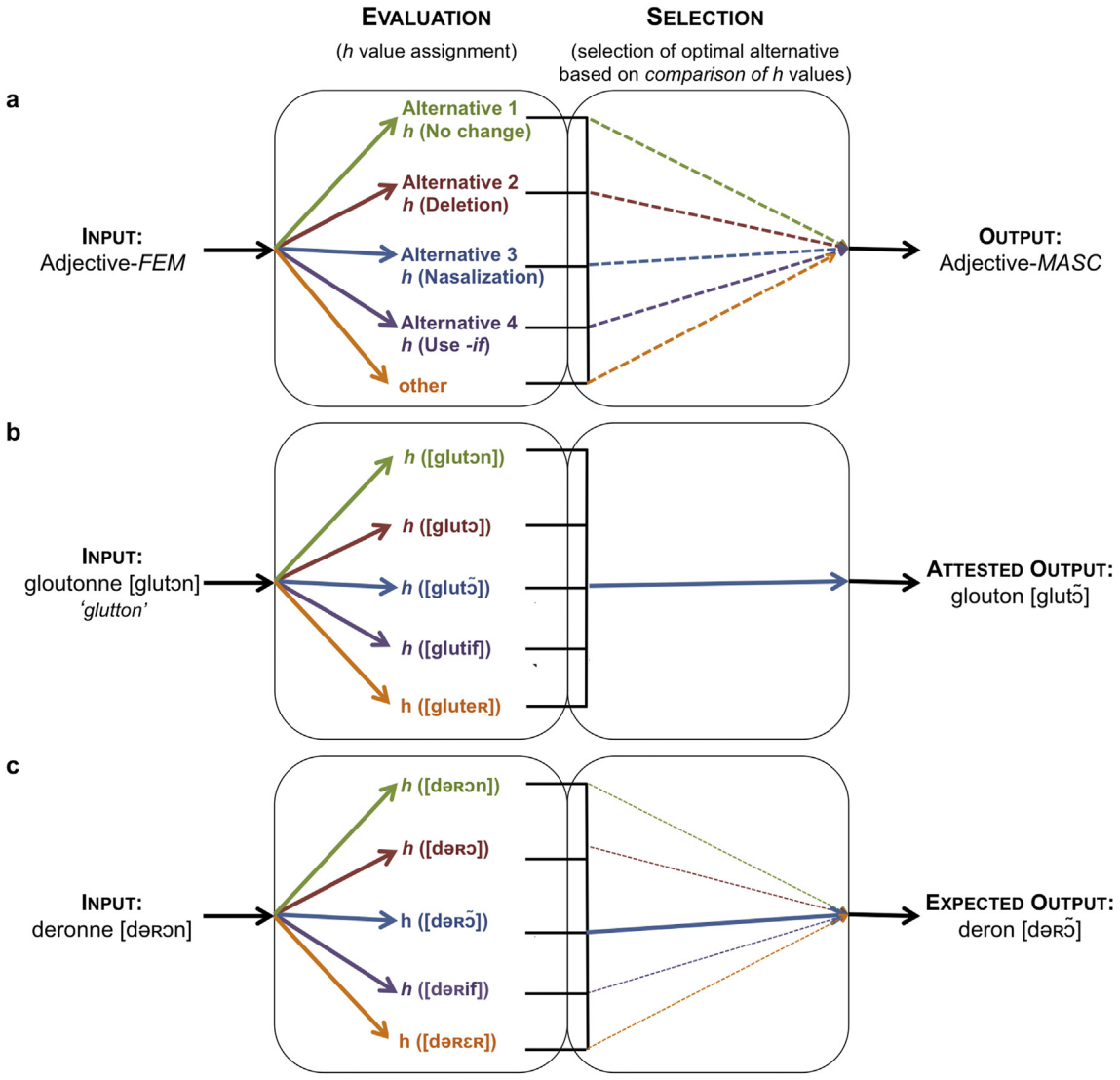

Fig. 1 – Description and model of the linguistic task. Model of the linguistic task with two distinct components (a). Given a feminine input, harmony values (*h*) are assigned to possible masculine alternatives in the Evaluation component. *Other* refers to the set of alternatives with low harmony values that could be generated by the grammar but would not be selected by the Selection component. In the Selection component, a masculine output is selected on the basis of these values. Derivation of a masculine adjective from its feminine counterpart, with an example from the French lexicon (*gloutonne*, 'glutton') (b). Example of a behavioral trial with the nonce adjective *deronne* (c). Text outside the brackets corresponds to the orthographic form; text in square brackets corresponds to the actual pronunciation of the form, transcribed using the International Phonetic Alphabet (IPA). The IPA symbols ə, ʀ and ɔ in [dəʀɔn] correspond respectively to the sound of the first vowel in *again* in American English, to the French sound for *r* and to the sound of the first vowel in *all* in American English. The diacritic ~ (as in [dəʀɔ̃]) indicates a nasal vowel.

group of subjects did not perform the behavioral task as it was only used to assess brain atrophy in our HD population.

All patients were evaluated with the UHDRS, which includes the Verbal Letter Fluency test (Cardebat, Doyon, Puel, Goulet, & Joanette, 1990), the Trial-Making Test A and B (TMT A and B) (Tombaugh, 2004), the Symbol Digit Modalities Test [SDMT (Wechsler, 1981)] and the Stroop interference test (Golden, 1978). Patients also completed the Mattis Dementia Rating Scale [MDRS (Mattis, 1976)]. Table 1 summarizes demographic and clinical data of the participants included in the analyses.

The study was carried out in accordance with the Declaration of Helsinki. Participants were recruited from an outpatient clinical biomarker program (NCT01412125) approved by the ethics committee of Henri Mondor Hospital (Créteil, France). The committee approved all parts of our experiments involving testing of patients and healthy controls. All participants gave informed consent.

Table 1 – Demographic and genetic information for HD patients, demographic data for controls, and results from the neurological and neuropsychological assessments of HD patients.

	Whole cohort of HD patients	Subgroup of HD patients with MRI	Controls	Group of Controls with MRI
N	30	25	30	25
Sex	15F/15M	12 F, 13 M	16F/14M	14F/11M
Age (years)	50.3 ± 8.8	50.8 ± 8.6	50.3 ± 10.7	50.4 ± 9.7
Years of education	13.5 ± 2.5	13.3 ± 2.5	14 ± 2.4	
Handedness	25R/5L	22R/3L	24R/6L	
N of CAG repeats[a]	44 ± 2.1	44 ± 2.6	–	
Disease burden score[b]	422.6 ± 82.2	395 ± 94.6	–	
N of years since disease onset	6.2 ± 4.2	6.7 ± 4.4	–	
			(normal values)*	
UHDRS TFC[c]	11.6 ± 0.7	11.8 ± 0.7	13	
UHDRS motor[c]	22.9 ± 13.1	22.5 ± 10.8	0	
Mattis Dementia Rating Scale	134.4 ± 9.3	134.8 ± 9.8	>136[d]	
Letter fluency	42.2 ± 22.2	46.4 ± 23.1	>45[e]	
Stroop interference	27.8 ± 8.6	28.6 ± 8.6	>35[f]	
Symbol digit code	31.1 ± 10.1	31.5 ± 9.5	>37[g]	
Trail-making test A (s)	57.3 ± 25.9	55.1 ± 21.9	<31[h]	
Trail-making test B (s)	127.6 ± 60.1	119.3 ± 56.9	<64[h]	

F = female, M = male, R = right-handed, L = left-handed.
[a]Number of CAG repeats in the *Htt* gene.
[b]Disease-burden score = age × (CAG length−35.5), Penney, Vonsattel, MacDonald, Gusella, and Myers (1997).
[c]UHDRS = United Huntington Disease Rating Scale, TFC = total functional capacity score, Huntington Study Group (1996).
*Normal values were obtained from: [d]Mattis (1976); [e]Cardebat et al. (1990) – values for 2 min for the 3 letters P, R and V; [f]Golden (1978), color/words; [g]Wechsler (1981); [h]Tombaugh (2004).

2.2. *Behavioral task*

2.2.1. *Stimuli and procedure*

Stimuli belonged to the four common alternation patterns present in the French lexicon [type frequency >100 per million (Bybee, 1995; New, Pallier, Ferrand, & Matos, 2001)] (alternatives 1–4 in Fig. 1a). The token frequency of the different patterns is 3.74 for No change, 3.82 for Deletion, 4.44 for Nasalization and .82 for Use –if. For each one of these patterns, one or more feminine ending types were chosen, for a total of eleven adjectival endings. For instance, Nasalization was instantiated by the feminine endings '*-ine*', '*-aine*', '*-une*', '*-onne*'. This was done to include the different lexical instantiations of each alternation pattern and ensure variability in the experimental material. Test items were nonce disyllabic adjectives to optimize the grammatical evaluation and selection components of the task, minimizing lexical effects. For each feminine ending type, fifteen nonce adjectives were created by adding, subtracting, or substituting two phonemes from an existing French adjective, for a total of 165 stimuli. The stimuli were matched for number of phonemes ($F > 1$) and consisted of legal phoneme strings that differed in at least two phonemes from any existing French word.

Participants were presented with a spoken sentence containing the relevant nonce adjective in the feminine form (*La fille est très* X-FEM, e.g., *La fille est très deronne*, 'the girl is very *deronne*-FEM'), and were asked to provide the sentence containing the corresponding masculine (*Le garçon est très* X-MASC, e.g., *Le garçon est très deron*, 'the boy is very *deron*-MASC'). Feminine forms were randomized for each participant. We familiarized participants to the task by training them with feedback. Practice items included real feminine adjectives and nonce adjectives.

Responses were categorized into four types (No change, Deletion, Nasalization, Use -if). Responses that matched the expected form were coded as correct; all other responses were coded as incorrect. For one of the eleven feminine ending types, "-te", two masculine responses were coded as correct, i.e., Deletion and No change, since both alternation patterns are attested in the French lexicon for these feminine forms (compare e.g., *petite*-FEM [pətit] – *petit*-MASC [pəti] 'small', and *tacite*-FEM [tasit] – *tacite*-MASC [tasit]), although the first one is much more frequent than the second one. As an example of how responses were coded, if the speaker heard *deronne*, the correct response, *deron*, would be considered to correspond to Nasalization, whereas the incorrect responses *deronne*, *dero* and *derif* would be coded as No change, Deletion, and Use –if errors, respectively; all other incorrect responses were coded as Aberrant (e.g., *derer*), (Fig. 1c).

2.2.2. *Data analysis*

R package *lme4* (Bates, Machler, Bolker, 2015) was used for statistical analyses. Linear mixed-effects models were used to analyze participants' responses. By-subject random intercepts and slopes were included. We evaluated the relationship between linguistic performance and the results of clinical assessment tests, and sociodemographic data, with Pearson's product-moment correlation analyses.

2.3. *Brain damage delineation*

2.3.1. *MRI data acquisition*

Brain MRI scans were obtained for twenty-five of our thirty HD patients and for twenty-five healthy controls matched for age and sex [t-test: $t_{48} = .22$, $p = .83$ and chi-square test: $\chi^2(1) = .32$,

$p = .57$, respectively, Table 1], to delineate gray matter (GM) atrophy in our HD population. All scans were acquired at Henri Mondor Hospital, on a Siemens Symphony 1.5T MRI scanner with a 12-channel head coil. A T1-weighted acquisition (MP-RAGE, TE/TR = 3.72/2400 msec, TI = 1000 msec, flip angle = 8°, acquisition matrix = 256*256, FOV = 256 × 256 mm, voxel size = 1 × 1 × 1 mm^3, sagittal sections: 160) was used to perform VBM analyses.

2.3.2. *MRI data analysis*

VBM data preprocessing and analysis were performed with VBM8 (http://dbm.neuro.uni-jena.de/vbm/), an SPM8 toolbox (http://www.fil.ion.ucl.ac.uk/spm) running on Matlab. Structural images were corrected for intensity bias, tissue-classified and registered, using linear and non-linear transformations (DARTEL), within a unified model (Ashburner & Friston, 2005). GM segments for each subject were modulated using non-linear components of the normalization only, thereby preserving actual tissue values locally, to take individual brain size into account globally. Modulated, normalized GM segments were smoothed with a 6-mm FWHM Gaussian kernel.

A full factorial design model assessed group differences in GM volume between control and HD patients with group as main factor and age as covariate. An average GM mask was created from the normalized GM segments of the twenty-five healthy controls, thresholded at a value of .20 (voxels with >20% GM fraction values). This mask was used to restrict statistical comparisons to the GM. Results were corrected for multiple comparisons using family-wise error (FWE-corrected, $p < .05$). Anatomical labeling of significant clusters was achieved using the AAL atlas implemented in MRIcro software (http://cnl.web.arizona.edu/mricro.htm). A binary mask was created by pooling the significant clusters in this group analysis, representing the areas of GM atrophy in HD patients (Fig. 3a,b). This mask was used for subsequent correlation analyses with behavioral data.

2.4. *Correlations between behavioral data and GM atrophy*

2.4.1. *Correlation analyses within the GM mask*

A multiple regression analysis explored the correlation between linguistic performance and whole brain GM volumes in HD patients, with education level as covariate. Statistical outcomes were observed with corrected *p*-values inferior to .05 using Family-Wise Error (FWE) and a minimum of 25 voxels per cluster.

2.4.2. *Correlation analyses within the mask of GM atrophy in HD patients*

A multiple regression analysis explored the correlation between linguistic performance and GM volumes in HD patients, restricted to regions showing atrophy in HD patients in comparison with controls, with education level as covariate. Statistical outcomes were observed with corrected *p*-values inferior to .05 using Family-Wise Error (FWE) and a minimum of 25 voxels per cluster.

The same analyses were conducted to investigate the correlation between GM volume and clinical scores [Stroop interference, SDMT, UHDRS motor score and disease burden score (Penney et al., 1997)].

2.4.3. *Correlation analyses with mean probability of GM in five striatal ROIs*

The striatum was manually segmented into five bilateral *a priori* anatomical masks (caudate body, caudate head, anterior putamen, posterior putamen and ventral striatum, including the nucleus accumbens). ROIs were defined for each hemisphere with MRIcro applied to the single-subject T1 template of SPM8 software as follows: The ventral striatum comprises all striatal voxels in which the demarcation between caudate and putamen is not visible; the anterior and posterior putamen comprise the putaminal voxels with 'y' coordinates higher and lower than zero, respectively; the caudate head

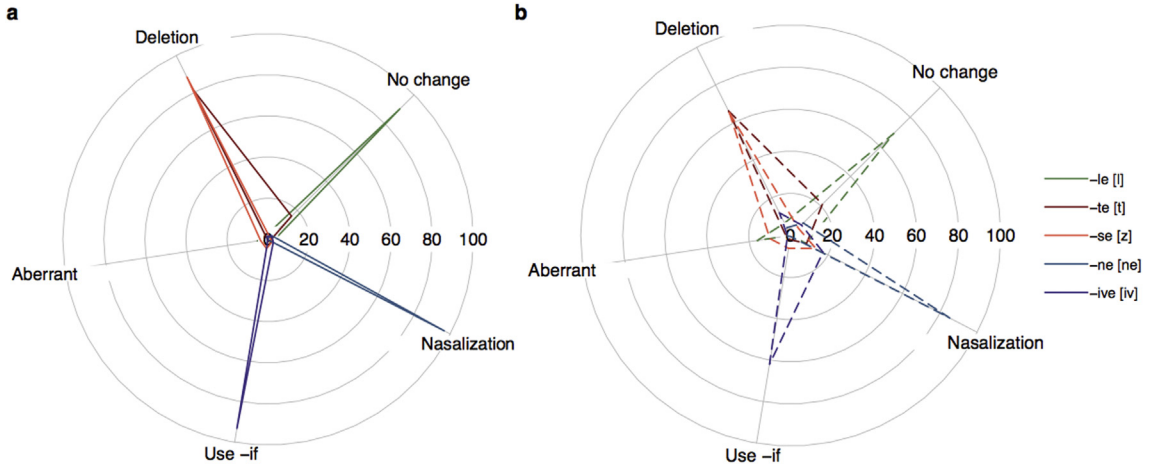

Fig. 2 – Behavioral responses. Response types provided by the subjects for the 5 feminine ending types (–*le* [l], –*te* [t], –*se* [z], –*ne* [n], –*ive* [iv]); Controls (a) and HD patients (b). Axes correspond to the types of response provided by the subjects; circles represent percentages.

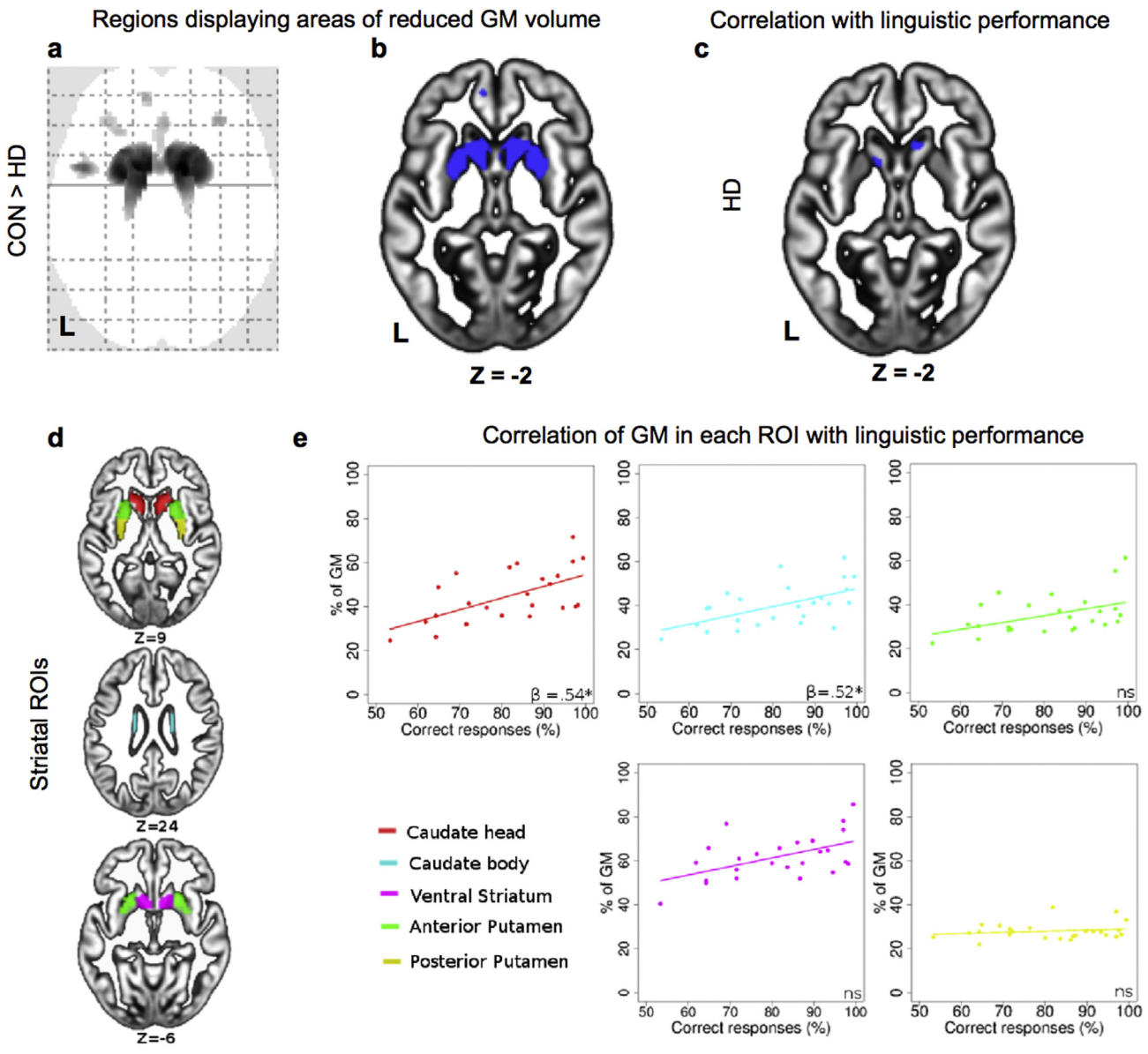

Fig. 3 – Neural correlates of linguistic performance in Huntington's Disease using VBM. Regions displaying areas of reduced GM volume (atrophy) in HD patients compared to controls (FWE, $p < .05$, corrected $t > 5.35$, extent cluster threshold set at 50 contiguous voxels), overlaid onto a glass brain (a). Binary GM mask of significant clusters from the group comparison (controls *vs* HD patients), overlaid onto the average template of GM of the twenty-five HD patients, built with the TOM8 toolbox (http://dbm.neuro.uni-jena/software/tom/) (b). Correlation between GM volume in the GM atrophy mask and linguistic performance in the twenty-five HD patients (FWE-corrected, $p < .05$), overlaid onto the average template of GM of the twenty-five HD patients; two clusters are identified, the right caudate nucleus (*x y z* coordinates of maxima in MNI space: 11 24 −2, cluster size: 40 voxels, T = 5.03) and the left caudate nucleus (*x y z* coordinates: −12 11 −3, cluster size: 35 voxels, T = 4.44) (c). Description of the five striatal ROIs overlaid onto the average template of GM (d). Results of the correlation analysis between the probability of GM in each ROI and linguistic performance, with the correlation coefficient β and * for $p < .05$ (e).

and body comprise the caudate voxels with 'y' coordinates higher and lower than zero, respectively (Douaud et al., 2006). The mean probabilities of GM found in these ROIs were extracted. Multiple linear regression analyses assessed the association of performance in the linguistic task with mean probability of GM in each bilateral striatal ROI, for all HD patients. Education level was used as covariate. Results were Bonferroni-corrected.

2.5. Computational modeling

2.5.1. Baseline model

The modeling process began with a phonological analysis of the French adjective system in MaxEntHG. In MaxEntHG, speech production consists of an evaluation stage and a selection stage. The evaluation stage begins with an input lexical representation (here, the feminine form of the adjective) and a small number of possible output pronunciations (potential masculine forms). Each input–output mapping is assessed by constraints. There are two types of constraints: faithfulness constraints, according to which the input should be similar to output, and markedness constraints, according to which the output should be simple to produce and to perceive. Constraints are associated with weights and the harmony of a mapping is the weighted sum of its constraint violations. Thus, the evaluation stage involves the assignment of harmony values to every possible mapping:

$$\text{Harmony}(i, o_j) = \mathring{a}_k w_k \cdot C_k(i, o_j), \quad [1]$$

where

i is the feminine form (the input) and o_j is a possible pronunciation of the masculine form (the output)
C_k is the k^{th} constraint, and $C_k(i, o_j)$ is the number of violations
w_k is the weight associated with C_k

In the selection stage, a particular output is selected with a probability proportional to its harmony:

$$\Pr(o_j|i) = \exp(\text{Harmony}(i, o_j))/Z_i, \quad [2]$$

where $Z_i = a^{\circ}{}_{j'} exp(Harmony(i, o_{j'}))$(a normalizing constant).

Thus, for a given constraint set and a given set of weights, Eq. (2) predicts a probability distribution over all outputs for each input.

The analysis involved choosing constraints that could yield the French adjectival system. We used eight standard phonological constraints. The optimal weights for a given set of data were determined by maximizing the likelihood of the data, according to Eq. (2) (assuming independence). The optimum was identified by gradient ascent, using the BFGS_B method in NumPy (Byrd, Lu, & Nocedal, 1995). Constraint weights of the baseline model were determined from the aggregate production data of the control population. The baseline model thus represents the behavior of a typical speaker, as estimated from the outputs produced by control participants.

2.5.2. Deficit models

It is convenient to write the evaluation and the selection steps in vector form, i.e., letting $w_{base} = [w_1, w_2, \ldots]$ and $\mathbf{C}(i, o_j) = [C_1(i, o_j), C_2(i, o_j), \ldots]$, where w_{base} represents the weights of the baseline model, as estimated above:

$$\text{Evaluation} \quad \text{Harmony}(i, o_j) = \text{wbase} \cdot \mathbf{C}(i, o_j)$$

$$\text{Selection} \quad \Pr(o_j¥i) = \exp(\text{Harmony}(i, o_j))/Z_i$$

We derived two classes of deficit models from these equations. In the evaluation deficit model, a speaker s is assumed to differ from the baseline model by the addition of a constant noise vector η_s drawn from a zero-centered Gaussian distribution with standard deviation η.

$$\text{Evaluation deficit} \quad \text{Harmony}_s(i, o_j) = (\mathbf{w}_{base} + \boldsymbol{\eta}_s) \cdot \mathbf{C}(i, o_j) \quad [3]$$

In the selection deficit model, a speaker s is assumed to differ from the baseline model in that the harmony is multiplied by a constant weakening factor λ_s, drawn from a uniform distribution over the interval [a, b], $0 \le a \le b \le 1$.

$$\text{Selection deficit} \quad \Pr_s(o_j|i) = \exp(\lambda_s \cdot \text{Harmony}(i, o_j))/Z_i \quad [4]$$

Thus, the evaluation deficit model has the 'noise level' η as a free parameter, and the selection deficit model has the 'weakening level' λ as a free parameter.

2.5.3. Simulation

Monte-Carlo method was used to derive predictions from a stochastic theory by explicitly simulating the stochastic process repeatedly. A *run* R proceeded as follows. First, thirty copies of the control grammar were produced (matched to the number of HD patients). Each copy was then perturbed according to the selection deficit or evaluation deficit above. Thus, every s models a typical speaker of French afflicted by either a selection deficit or an evaluation deficit. Within a run, every s has the same deficit. All thirty s's perform the same task as HD patients, generating masculine adjective forms from the feminine forms, according to the distributions generated by Eqs. (1)–(4). Outputs from each speaker s within the run are aggregated, yielding a sample from the predicted distribution (for the selection or evaluation distribution, depending on the run), with $Fr_R(o_j|i)$ representing the total number of times the masculine form o_j was produced for feminine form i. The *log probability* of a run R is determined by Eq. (5):

$$L(R) = \sum_{(i,j)} Fr_R(o_j|i) \ln \Pr_{HD}(o_j|i) \quad [5]$$

Conditional probabilities $\Pr_{HD}(o_j|i)$ in Eq. (5) are estimated from the HD patient data using add-one smoothing, e.g., $\Pr_{HD}(o_j|i) = [1 + Fr_{HD}(i, o_j)]/[\Sigma_k\, 1 + Fr_{HD}(i, o_k)]$. The log probability of a run is a relative measure of how much the sample output distribution (selection or evaluation deficit) resembles the actual output distribution from HD patients. One thousand runs were conducted with each deficit model.

The deficit models were assessed by determining which one assigned higher probability to the data. On individual runs, either the evaluation or the selection deficit model might assign higher data likelihood, indicating that the ability to account for the data was not baked into either. Nonetheless, the selection deficit model provided a better fit to the data on an average run, indicating it is a closer match to HD patients' speech production process.

Table 2 – Distribution of participants' responses for each alternation. Lines correspond to the different feminine ending types. Columns correspond to the alternation pattern used by participants to produce the masculine form. Shaded cells correspond to responses coded as 'correct', non-shaded cells correspond to cells coded as errors (for the ending type "–te" see the stimuli description in the Material and Methods section). Numbers in each line correspond to percentages out of the total number of responses, across participants (Controls, left and HD patients, right). Feminine and masculine forms are provided according to the French orthography (in italics) and according to the International Phonetic Alphabet (IPA) (in square brackets), which correspond to the actual pronunciation of the form.

		Response type (%)				
		No change	Deletion	Nasalization	Use -if	Aberrant
Feminine ending type	**-le [-l]** *nurfale* [nyʀfal]	90.18/68.89 *nurfale* [nyʀfal]	2.13/6.56 *nurfa* [nyʀfa]	2.45/8.44 *nurfan* [nyʀfɑ̃]	.00/.00 *nurfif* [nyʀfif]	5.24/16.11 *nurfo* [nyʀfo]
	-te [-t] *spamite* [spamit]	16.04/21.22 *spamite* [spamit]	81.07/66.11 *spami* [spami]	1.22/8.45 *spamin* [spamɛ̃]	1.33/2.00 *spamif* [spamif]	.34/2.22 *spamol* [spamɔl]
	-se [z] *stopise* [stopiz]	1.22/5.00 *stopise* [stopiz]	88.18/65.28 *stopi* [stopi]	2.34/13.46 *stopin* [stopɛ̃]	4.56/6.22 *stopif* [stopif]	3.70/10.04 *stoper* [stopɛʀ]
	-ne [n] *polune* [polyn]	2.50/8.40 *polune* [polyn]	.50/4.12 *polu* [poly]	96.61/85.25 *polun* [polɔ̃]	.22/.50 *polif* [polɔif]	.17/1.73 *polsane* [polsan]
	-ive [iv] *merive* [məʀiv]	2.44/7.11 *merive* [məʀiv]	1.56/12.00 *meri* [məʀi]	2.89/17.33 *merin* [məʀɛ̃]	93.11/62.00 *merif* [məʀif]	.00/1.56 *merta* [məʀta]

3. Results

3.1. Behavioral results

HD patients performed worse than controls [76.4% and 89.9% accuracy, respectively ($F_{1, 58} = 4.77$, $p < .05$)]. Table 2 illustrates the distribution of responses for each alternation included in the experiment.

As Fig. 2 shows, HD patients followed the same response pattern as Controls, but more noisily. We found an interaction between subject group and error type [$F_{4, 232} = 3.64$, $p < .01$], due to a combination of two factors, as shown by two *post-hoc* analyses. First, HD patients made errors concerning the most frequent alternation patterns in the French lexicon more frequently than controls [$F_{1, 177} = 9.27$, $p < .01$]. For instance, HD patients were more likely to produce a Nasalization error (e.g., nurfale – nurfan), where the lexical token frequency is 4.4 *per million words* (New et al., 2001), than a Use-if error (e.g., nurfale – nurfif), where the Use-if alternation is less frequent in the French lexicon (token frequency = .83 *per million words*). Second, HD patients perseverated more than controls. A perseverative error was defined as an error due to the erroneous application of the same alternation pattern as the one given in the previous two trials (HD patients: mean = 5.3, controls: mean = 3.8, $p < .05$). These perseverations were not due to the fact that randomization yielded a greater number of consecutive trials in HD patients than in controls. In fact the difference between then two groups was restricted to perseveration errors but there was no difference between groups for correct consecutive responses of the same type (HD patients: mean = 4.13, controls: mean = 4.03, $p = .7$).

Performance in the linguistic task was correlated with level of education in HD patients and controls, and with the CAG repeat length and the UHDRS motor score in HD patients. Linguistic performance of HD patients was also correlated with the MDRS memory and attention scores, with the Stroop interference score, the SDMT, Verbal Letter Fluency and TMT A and B (Table 3).

3.2. Brain damage delineation

The between-group VBM analysis revealed reduced GM volume in HD patients as compared to healthy controls, in the basal ganglia (caudate nucleus and putamen, bilaterally, and right globus pallidus) and the frontal cortex (precentral and orbital) (Fig. 3a, Table 4). No significant increase in regional GM volume was found in HD patients relative to controls. A binary GM mask including significant clusters for this group effect (Controls *vs* HD patients, CON > HD) was built (Fig. 3b) for subsequent analyses of correlations with behavioral data.

3.3. Correlations between linguistic performance and GM atrophy

Multiple regression analyses explored the correlation between accuracy in the linguistic task and GM volume in the twenty-five HD patients who underwent structural MRI. Like the whole cohort, these patients responded less accurately than their matched controls [79.8% and 89.9% correct responses, respectively ($F_{1, 53} = 4.11$, $p < .05$)]. See Table 3 for correlation analyses with demographic and neuropsychological data.

3.3.1. Correlation analyses within the GM mask

The correlation analysis on the whole brain did not reveal any correlation between GM regions, cortically and subcortically, and accuracy in the linguistic task.

3.3.2. Correlation analyses within the mask of GM atrophy in HD patients

The analysis was restricted to the GM mask obtained from the between-group comparison (CON > HD, Fig. 3a and b. A positive correlation was found between accuracy in the linguistic task and GM volume in the bilateral caudate nucleus of HD patients (FWE-corrected, $p < .05$) (Fig. 3c), but not in the frontal areas. Scores of executive function tests (SDMT and Stroop) did not correlate with GM volume within the striatum. The SDMT correlated with GM volume in the inferior orbitofrontal

Table 3 – Results of the partial correlation analyses between linguistic performance and demographic data, clinical and cognitive assessment and genetic measurements, and the results of a Welch two-sample t-test for sex (degrees of freedom in parentheses).

	Linguistic performance		
	Whole cohort of HD patients	Subgroup of HD patients with MRI	Controls
Demographic data			
Age	n.s.	n.s.	n.s.
Years of education	.48***(57)	.36**(52)	.48***(57)
Sex	n.s.	n.s.	n.s.
General assessment			
UHDRS motor[a]	−.44* (27)	−.64*** (23)	–
UHDRS TFC[a]	n.s. (28)	n.s. (23)	–
N of CAG repeats[b]	−.55** (26)	−.46* (19)	–
Disease burden score[c]	−.46* (26)	−.46* (19)	–
N of years since disease onset	n.s. (24)	n.s. (18)	–
Cognitive assessment			
MDRS memory[d]	.79*** (27)	.83*** (20)	–
MDRS attention[d]	.66*** (27)	.66** (20)	–
Letter fluency[e]	.62*** (27)	.67*** (20)	–
Stroop interference[f]	.69*** (27)	.63** (22)	–
Symbol digit code[g]	.65*** (27)	.72*** (23)	–
Trail-making test A[h] (s)	−.38* (27)	−.47* (20)	–
Trail-making test B[h] (s)	−.62*** (27)	−.59** (20)	–

n.s. = non-significant ($p > .05$); *$p < .05$; **$p < .01$; ***$p < .001$.
[a] UHDRS = United Huntington Disease Rating Scale, TFC = total functional capacity score, Huntington Study Group (1996).
[b] Number of CAG repeats in the *Htt* gene.
[c] Disease-burden score = age × (CAG length−35.5), Penney et al. (1997).
[d] Mattis Dementia Rating Scale, Mattis (1976).
[e] Cardebat et al. (1990) – values for 2 min for the 3 letters P, R and V.
[f] Golden (1978), color/words.
[g] Wechsler (1981).
[h] Tombaugh (2004).

Table 4 – Results of voxel-based analysis for assessing regional GM differences between controls and Huntington's Disease patients, with age as a covariate (FWE-corrected, $p < .05$).

Anatomical region	Side	Cluster size N voxels	T	MNI coordinates (x y z, mm)		
Basal ganglia						
Caudate nucleus (head)	L	2782[a]	10.64	−12	9	−3
Putamen			10.25	−21	5	7
Caudate nucleus (body)			9.89	−9	0	13
Globus Pallidus	R	3064[a]	10.93	14	9	−6
Putamen			9.81	23	5	7
Caudate nucleus (body)			9.78	12	5	16
Frontal cortex						
Precentral gyrus	L	201	8.25	−44	8	30
Medial Orbital		52	6.50	−8	51	−5
Superior Orbital		99[a]	6.09	−23	30	−17
Inferior Orbital			5.89	−29	36	−15
Inferior Orbital	R	53	6.76	36	38	−12
Medial Orbital		112[a]	6.44	3	36	−12
Olfactory			5.78	2	24	−12

[a] Indicates contiguous clusters. Only clusters larger than 50 contiguous voxels are reported.

gyrus, bilaterally (FWE-corrected, $p < .05$). Conversely, the UHDRS motor score correlated bilaterally with GM volume in both the putamen and the caudate nuclei, and the disease burden score was negatively correlated with GM volume in the right caudate nucleus (FWE-corrected, $p < .05$).

3.3.3. *Correlation analyses with mean probability of GM in five striatal ROIs*

Among the five striatal regions of interest (ROIs) (Fig. 3d), accuracy in the linguistic task only correlated with the mean probability of GM in the caudate heads and the caudate bodies

(respectively $\beta = .54$, $p < .05$ and $\beta = .52$, $p < .04$, Bonferroni-corrected, Fig. 3e). No neuropsychological or clinical score correlated with GM in the five ROIs, apart from the UHDRS motor score, which negatively correlated with caudate head ($\beta = -.51$, $p < .05$), anterior putamen ($\beta = -.59$, $p < .01$) and ventral striatum ($\beta = -.66$, $p < .01$).

3.4. *Computational results*

There was a linear relationship between the log frequency of HD patients' responses and the responses of controls for the same feminine-masculine adjective pair ($R^2 = .87$). This suggests that a log-linear model is suited to model the alternation, since in log-linear models the probability of generating an item is proportional to the exponential of some score function. As the correlation is quite strong in the log domain, it suggests that the score function for HD patients is 'close' to the score function for controls, i.e., HD can be understood as applying some simple transform to the score function. Since in the field of morpho-phonology, a log-linear model OT-based model called MaxEntHG already exists and many properties of the scoring function are understood, it was used to model the alternation. MaxEntHG allows one to separate the process of attributing values to masculine output options from the process of selecting amongst masculine outputs, by capturing them with different parameters.

We first determined the constraint weights of the baseline model by maximizing the likelihood of the aggregated production data for the control population. We then derived two classes of deficit models from the baseline model. In the evaluation deficit model, a speaker *s* is assumed to differ from the baseline model by the addition of a constant noise vector η_s. In the selection deficit model, a speaker *s* is assumed to differ from the baseline model in that the harmony is multiplied by a constant weakening factor λ_s. The 'best' values for η and λ were determined empirically by trying a variety of values. The values which assigned the greatest likelihood on average to the HD patient data were $\eta = .9$ and $\lambda = .6$.

Monte-Carlo method was used to derive predictions from a stochastic theory by explicitly simulating the stochastic process repeatedly. One thousand runs were conducted with each deficit model. Outputs from each speaker *s* within the run were aggregated and the log probability of each run was determined. Results show that the selection deficit model accounts significantly better for the data (mean log likelihood −3867.81, median −3864.53; heteroscedastic *t*-test $t_{1005} = -22.27$, $p < .001$) than the evaluation deficit model (mean log likelihood −3909.08, median −3902.66).

4. Discussion

We investigated the mechanisms underlying language impairment in patients with striatal lesions, using HD as a model. Moving beyond phenomenological descriptions of the impairment, we used behavioral, imaging and modeling methods to investigate the computational mechanisms of language processing. This approach allowed us to test a new hypothesis of the role of the striatum in language and thus to propose a new theory of the source of language impairment in striatal lesions.

Patients with early HD performed worse than their matched controls in the linguistic task. Their accuracy (76.4%) was comparable to the one reported by previous studies testing morphological abilities in these patients [e.g., ca. 75% in (Teichmann, Dupoux, Kouider, & Bachoud-Levi, 2006)]. This poor performance was associated with reduced striatal volume, as revealed by the VBM analysis. Patients produced errors falling in the four standard patterns for French adjectives. This response pattern was qualitatively similar to the one of control participants. Quantitatively, however, it was different, in that the number of selected non-optimal alternatives was higher. Our behavioral result thus indicates that the core grammatical component responsible for generating the possible masculine outputs is spared in HD patients.

The observed similarity between the two response patterns is problematic for theories assigning the striatum a role in the computation of linguistic rules (Nemeth et al., 2012; Teichmann et al., 2005, 2006, 2008; Ullman, 2006; Ullman et al., 1997). If HD patients had a core grammatical deficit, we would expect them to produce responses that are incompatible with the grammar of French (i.e., responses of the type Aberrant), contrary to fact.

Our computational analysis using MaxEntHG sheds light on the specific nature of the deficit in HD. Provided that the chosen computational model and its parameters are accurate abstractions of language production mechanisms in humans, these modeling results support the hypothesis that the language deficits observed in patients are caused by a selection deficit rather than by an impairment of underlying grammatical knowledge. We showed that the noisier distribution of responses following striatal damage can be captured specifically, by introducing randomness in the selection process (simulated by the selection deficit model). By contrast, introducing noise in the harmony calculation (simulated by the evaluation deficit model) yielded a poor fit to the patients' data.

Our modeling results are consistent with the notion that, even in language processing, the striatum is responsible for processing the outcomes of the evaluation component, to favor the more frequent selection of the best option, as suggested in studies of reinforcement and punishment learning (O'Doherty et al., 2004; Palminteri et al., 2012).

OT allows us to disentangle two distinct processes occurring during language processing: grammatical evaluation and selection. We are now able to unveil the mechanisms giving rise to apparently incongruent results collected with HD patients tested on morphological tasks (Nemeth et al., 2012; Teichmann et al., 2005, 2006, 2008; Ullman, 2006; Ullman et al., 1997). In fact, the error pattern induced by a selection deficit will depend on the specific properties of the morphological paradigm used to test patients. In English, for instance, there is only one default regular alternation for the past tense. Since the irregular patterns in English are not comparable in their frequency and in their scope to this one regular alternative (Albright & Hayes, 2003), a selection deficit will result in an abnormal rate of selection of the *–ed* pattern. This is in line with what was observed by Ullman and colleagues (Ullman et al., 1997). More recently, Nemeth and colleagues observed a similar over-regularization pattern in pre-manifest HD subjects tested on the inflection of irregular nouns in Hungarian (Nemeth et al., 2012). Irregular nouns in Hungarian

belong to a very restricted class. Alternations within this class are therefore not comparable in terms of frequency and scope to the regular ones. Like in the English past tense paradigm, an incipient selection deficit in this population would thus more likely result in the erroneous selection of the regular alternative instead of the irregular one (i.e., over-regularization error), than in the opposite error pattern. French, by contrast, has two regular alternations for the formation of the future tense (first conjugation and second/third conjugation). The default pattern is also the most frequent one. In addition French also has a variety of highly restricted irregular alternatives (Meunier & Marslen-Wilson, 2004) that have a low probability of being considered as part of the set of possible alternatives being considered for each given nonce verb. A patient with a selection deficit would most likely select the default alternative (i.e., first conjugation) for items belonging to the less frequent conjugation class. HD patients will also produce the reverse error pattern – though to a lesser extent – i.e., they will select the less frequent alternative instead of the most frequent one. In fact, this is in line with the response pattern found by Teichmann and colleagues (Teichmann et al., 2005, 2006, 2008).

Our paradigm, with four possible and equally regular alternatives, allows us to show that previously observed error patterns looked as if they were due to a grammatical deficit, because of the specific properties of the morphological paradigms. We could recover the mechanisms through which controls perform the task and compare them to the patients', because we have access to the error pattern of the control population. This was possible because our task was significantly harder than previously used tasks and did not yield ceiling performance in control subjects.

Recently it has been proposed that linguistic operations involving movement such as sequential and hierarchical processing in syntax or lexico-semantic mapping of movement in action verbs, are subserved by the frontostriatal network that coordinates motoric information (Birba et al., 2017). Within this neuronal recycling framework (Dehaene & Cohen, 2007), the different substructures of the striatum may play distinct roles in linguistic operations requiring movement, e.g., with the substantia nigra being involved in functional role assignment (Garcia et al., 2017). In our study, we focused on a linguistic process – a morphological alternation – which is not based on movement but on the evaluation and selection of linguistic alternatives and showed that it relies on the caudate.

Our proposal that the striatum holds a role in the selection of linguistic alternatives provides a new framework to reconsider further previous findings of a striatal implication in a coherent way. For instance, research on syntactic processing proposes that the striatum is recruited for syntactic reanalysis, for the resolution of ambiguities and for selecting references in the discourse (Hinzen et al., 2017; Kotz et al., 2003; Mestres-Misse et al., 2012; Sambin et al., 2012). In all of these studies, the role of the striatum can be reinterpreted as one pertaining to the selection of one among several syntactic parses. Similarly, in lexical processing the proposed role of the striatum in the inhibition among competing alternatives (Copland et al., 2003; Garcia et al., 2017; Longworth et al., 2005) can be restated as a role in the selection among alternatives. A selection deficit could also be at the origin of the rule-learning deficit observed in early HD patients (De Diego-Balaguer et al., 2008), since learning an artificial language requires not only the extraction of regularities from the speech stream, but also the selection of the abstract rule which best characterizes the language to be learned. Finally, our proposal can also account for neuroimaging studies of healthy subjects showing striatal activation in tasks requiring monitoring and controlling the language in use in bilingual speakers (Crinion et al., 2006; Friederici, 2006), as these tasks also involve selecting among several available linguistic constructions.

The correlation analysis within the five striatal subregions allowed us show that linguistic performance was not correlated indiscriminately with atrophy in any striatal region. Within the dorsal striatum, the correlation between GM atrophy and linguistic performance was statistically predominant in the caudate nucleus. This result is consistent with the fact that this striatal sub-territory receives projections from the lateral frontal cortex and Broca's area (Alexander et al., 1986). Atrophy in the caudate nuclei thus undermines the selection process in the linguistic domain. This impairment results in the more frequent selection of suboptimal outcomes (i.e., outcomes with low harmony scores) than in healthy controls.

The model used here is necessarily different from those adopted in, e.g., reinforcement learning studies [e.g., Q-learning models (Sutton & Barto, 1998)], because it was developed in the field of computational linguistics, which deals with very different objectives and modeling constraints. Despite these differences, comparisons across cognitive domains can be fruitfully established, provided equivalent parameters can be identified across the different models. Specifically, the 'deficit' that can be captured by modifying the selection parameter λ of our linguistic MaxEntHG is computationally equivalent to the 'deficit' that can be introduced by modifying the choice randomness parameter in a punishment-learning model (Palminteri et al., 2012).

Within the broader perspective of the language network, the relationship between cortical language areas and the striatum is analogous to that identified in other domains, between cortical areas and structures of the basal ganglia. The striatum operates as a centralized selection mechanism choosing between alternative options which are assigned weight values in designated connected cortical areas (Alexander et al., 1986; Redgrave, Prescott, & Gurney, 1999), Fig. 4. For instance, in the motor domain, the putamen selects between weighted motor programs evaluated by connected cortical premotor areas (Alexander et al., 1986; O'Doherty et al., 2004). A different corticostriatal circuit is responsible for behavioral goals, that are weighted and assigned reward values in the orbito-frontal cortex and selected by the ventral striatum (Hare et al., 2008; Kable & Glimcher, 2009; Montague & Berns, 2002; Padoa-Schioppa & Assad, 2008; Rangel et al., 2008). We propose that, through a parallel mechanism, linguistic alternatives evaluated in the left frontal and temporal cortices are selected within the caudate nucleus via the fiber tracts connecting these cortical areas with this subcortical structure.

Extensive studies are required to investigate corticostriatal dynamics within the language network. Our proposal is however already supported anatomically by tractographic

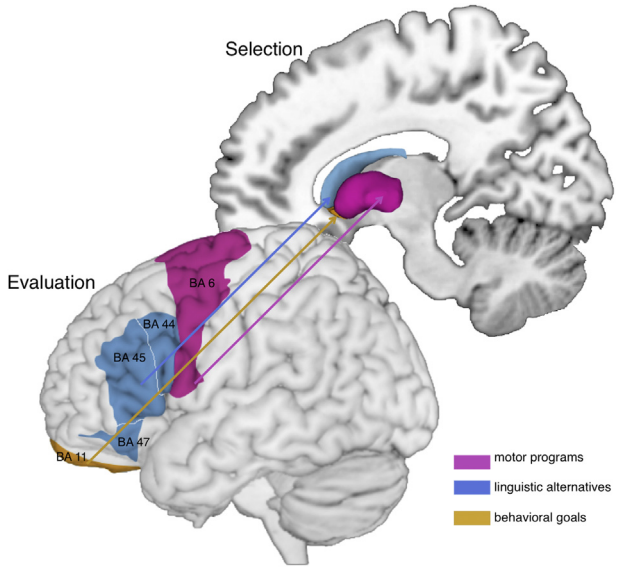

Fig. 4 – Schematic representation of evaluation and selection processes through corticostriatal pathways. Neural correlates of Evaluation processes (bottom left): Frontal cortical regions recruited during language processing (BA 44 and 45, which form Broca's Area, and BA 47) – shaded in blue – are involved in the assignment of weight values (harmony values) to linguistic alternatives. Premotor areas (BA 6) involved in the assignment of weight values to motor programs are shaded in pink. The orbito-frontal cortex (BA 11), which assigns weight values to behavioral goals, is shaded in yellow. These cortical areas are connected to striatal subregions (top right) through corticostriatal connections represented schematically by arrows of the corresponding color. The blue arrow represents the pathway linking frontal language regions to the caudate nucleus (shaded in blue), the pink arrow represents the pathway linking premotor regions to the putamen (shaded in pink), the yellow arrow represents the pathway linking orbito-frontal areas to the ventral striatum (shaded in yellow). These striatal subregions are recruited for the Selection of the weighted options through a parallel mechanism: the caudate nucleus selects linguistic alternatives based on the assigned harmony values, the putamen selects among motor plans based on the assigned weighted values, the ventral striatum selects among behavioral goals based on the assigned reward values. (Abbreviations: BA = Brodmann area).

research mapping corticostriatal connections in the human brain, in both healthy subjects and brain lesioned patients. This research has identified connections between the caudate nucleus and Broca's area (BA 44, 45) (Draganski et al., 2008; Ford et al., 2013; Lehericy et al., 2004; Teichmann et al., 2015). Moreover, recent results on the modification of corticostriatal connections in HD have shown a decrease in bilateral connections from frontal areas to the dorsal striatum (Marrakchi-Kacem et al., 2013). Among the degenerated connections are the ones linking the caudate nucleus with BA 44, 45 and 47. This degeneration may provide the basis for the language impairment observed in patients with early HD in the present study. Recent reservoir computing models reflecting the contribution of frontal-striatal circuits in language processing (Hinaut & Dominey, 2013; Szalisznyo, Silverstein, Teichmann, Duffau, & Smits, 2017) have built on the brain connectivity literature to model the processing of complex syntactic structures and of thematic role assignment within a recurrent network of structurally segregated frontal-striatal circuits. Although both the computational models and the level of linguistic processing are very distinct from the focus of the present study, future research will have to explore to what extent the two lines of research make similar or different predictions – and test them both from a behavioral and from a computational perspective.

In addition, other brain regions, e.g., the anterior insula and the ventro-lateral prefrontal cortex have been reported to be involved in selection processes occurring post semantic retrieval, which resolve competition between simultaneously active representations. Activity in these areas was observed during the selection of words (e.g., in verb generation, confrontation naming, word recognition) or visual patterns (Badre & Wagner, 2005, 2007; Bourguignon, Ohashi, Nguyen, & Gracco, 2018; Kan & Thompson-Schill, 2004; Thompson-Schill et al., 1998). The relative specificities of the different selection mechanisms and their possible connections remain to be elucidated.

Finally, we investigated here the mechanism by which a specific type of linguistic alternatives is selected. Given the generality of the selection mechanism, it seems likely that the dorsal striatum, particularly the caudate nucleus, plays a similar role for other language components. Furthermore, the observed parallelism between results from within and outside the domain of language raises questions about computational equivalence across domains. We are now in a position to address these questions.

Declaration of interest

The authors declare no conflict of interest.

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