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The role of the striatum in sentence processing: Disentangling syntax from working memory in Huntington's disease

Sara Sambin [a,b,c,1], Marc Teichmann [a,b,c,1], Ruth de Diego Balaguer [a,b,c,e], Maria Giavazzi [a,c], Dominique Sportiche [c,f,g], Philippe Schlenker [c,g,h], Anne-Catherine Bachoud-Lévi [a,b,c,d,*]

[a] INSERM U955, Equipe 1, Neuropsychologie Interventionnelle, IMRB, Créteil 94000, France
[b] Université Paris-Est, Faculté de médecine, Créteil 94010, France
[c] Ecole Normale Supérieure, Département d'Etudes Cognitives, Paris, France
[d] AP-HP, Hôpital H. Mondor – A. Chenevier, Centre de référence maladie de Huntington, Service de neurologie, 54 avenue du Maréchal de Lattre de Tassigny, Créteil 94000, France
[e] ICREA, Universitat de Barcelona, Departament de Psicologia Bàsica, IDIBELL, Barcelona, Spain
[f] UCLA, Department of Linguistics, LA, USA
[g] Institut Jean-Nicod, CNRS, Paris, France
[h] New York University, Department of Linguistics, NY, USA

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The role of sub-cortical structures in language processing remains controversial. In particular, it is unclear whether the striatum subserves language-specific processes such as syntax or whether it solely affects language performance via its significant role in executive functioning and/or working memory. Here, in order to address this issue, we attempted to equalize working memory constraints while varying syntactic complexity, to study sentence comprehension in 15 patients with striatal damage, namely Huntington's disease at early stage, and in 15 healthy controls. More particularly, we manipulated the syntactic relation between a name and a pronoun while holding the distance between them constant. We exploited a formal principle of syntactic theory called Principle C. This principle states that whereas in a sentence such as "Paul smiled when he entered" Paul and he can be a single person, this interpretation is blocked in sentences such as "He smiled when Paul entered". In a second experiment we varied working memory load using noun-adjective gender agreement in center-embedded and right-branching relatives (e.g., "the girl who watches the dog is green" vs. "the girl watches the dog which is green"). The results show that HD patients correctly establish name-pronoun coreference but they fail to block it when Principle C should apply. Furthermore, they have good performance with both center-embedded and right-branching relatives, suggesting that their difficulties in sentence comprehension do not arise from memory load impairment during sentence processing. Taken together, our findings indicate that the striatum holds a genuine role in syntactic processing, which cannot be reduced to its involvement in working memory. However, it only impacts on particular aspects of syntax that may relate to complex computations whereas other operations appear to be preserved. Hypotheses about the role of the striatum in syntactic processing are discussed.

1. Introduction

Language processing has mainly been ascribed to cortical areas, but several lines of research suggest that it also involves sub-cortical gray matter such as the striatum. A first indication of a role of sub-cortical areas in language processing was provided by patient studies showing that striatal damage leads to difficulties both with the production and with the comprehension of words and sentences (e.g., Cambier, Elghozi, & Strube, 1979; Damasio, Damasio, Rizzo, Varney, & Gersh, 1982; Hochstadt, 2009; Kumral, Evyapan, & Balkir, 1999; Lieberman et al., 1992; Teichmann et al., 2005; Ullman et al., 1997). However, it is still a matter of debate whether the striatum subserves genuine language processes, or whether it merely has a role in more general cognitive operations which modulate language processing (Caplan & Waters, 1999; Colman et al., 2009; Grossman, Carvell, Stern, Gollomp, & Hurtig, 1992; Grossman et al., 2000; Grossman,

* Corresponding author. AP-HP, Hôpital H. Mondor – A. Chenevier, Centre de référence maladie de Huntington, Service de neurologie, 54 avenue du Maréchal de Lattre de Tassigny, Créteil 94000, France. Tel +33 149813793; fax: +33 149812326.
E-mail address: bachoud@gmail.com (A.-C. Bachoud-Lévi).

[1] Both authors equally contributed to the paper.

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Lee, Morris, Stern, & Hurtig, 2002; Hochstadt, 2009; Hochstadt, Nakano, Lieberman, & Friedman, 2006; Lieberman, Friedman, & Feldman, 1990; Longworth, Keenan, Barker, Marslen-Wilson, & Tyler, 2005). Here, we address the question whether the striatum holds a genuine role in linguistic processing, independently from working memory, using the model of Huntington's disease.

Neurolinguistic research on sub-cortical structures has provided robust evidence that the striatum influences the processing of sentences. On the one hand, this impact is thought to be related to different non language-specific mechanisms such as the transient maintenance of word and phrasal information (Caplan & Waters, 1999; Grossman et al., 1992, 2000, 2002), the control and inhibition of competing alternatives (Longworth et al., 2005), the ability to switch from canonical to non-canonical word order depending on mechanisms of set-switching (Hochstadt, 2009; Hochstadt et al., 2006), and the recruitment of attentional resources (Grossman, 1999). On the other hand, it has been suggested that the striatum also holds a more specific role in language processing that cannot be reduced to executive functions or working memory. Ullman (2001) has proposed that striatal structures, and more generally frontal-striatal loops, subserve the processing and/or the knowledge of grammar such as the application of syntactic and conjugation rules (Teichmann, Dupoux, Cesaro, & Bachoud-Levi, 2008; Teichmann, Dupoux, Kouider, & Bachoud-Levi, 2006; Teichmann et al., 2005; Ullman, 2001; Ullman et al., 1997). Similarly, Friederici, Ruschemeyer, Hahne, and Fiebach (2003) and Kotz, Frisch, von Cramon, and Friederici (2003) have proposed that the striatum intervenes in late stages of integration between grammatical and semantic information (Friederici & Kotz, 2003; Kotz et al., 2003).

Such proposals are drawn from both imaging and behavioural studies in patients suffering from stroke and degenerative diseases. Patients with striatal stroke display various grammatical disorders affecting both the comprehension of complex sentences and the production of syntactically well-formed structures (Copland, Chenery, & Murdoch, 2000; Kumral et al., 1999; Pickett, Kuniholm, Protopapas, Friedman, & Lieberman, 1998). Sentence processing and conjugation difficulties have also been documented in degenerative diseases such as Huntington's disease (HD) (Illes et al., 1989; Jensen, Chenery, & Copland, 2006; Podoll, Caspary, Lange, & Noth, 1988; Teichmann et al., 2005; Ullman et al., 1997), characterized by primary neural death in the striatum, and Parkinson's disease (PD) (Geyer & Grossman, 1994; Grossman et al., 2000, 2002; Hochstadt et al., 2006), which is related to a dopaminergic deficit in striatal structures. Within the imaging literature, the use of event-related potentials has shown that patients with vascular and degenerative lesions of the striatum lack the modulation of an electrophysiological component which reflects syntactic integration and repair during sentence comprehension (Friederici & Kotz, 2003; Kotz et al., 2003). Furthermore, functional MRI studies with healthy participants have shown that violations of expectations of grammatical categories (e.g., "The ice cream was in the *eaten") activate the left striatum and Broca's area (Friederici et al., 2003). Likewise, in a PET imaging study, Moro et al. (2001) reported an activation of the left striatum and Broca's region for syntactic violations due to noun-determiner inversion.

In order to better define the function of the striatum in syntactic processing, several authors have focused on a specific computation, syntactic movement, since its impairment appears to be a core deficit in agrammatic patients (Burchert, Meissner, & De Bleser, 2008; Garraffa & Grillo, 2008; Grodzinsky, 2000). Syntactic movement takes place in sentences such as passives (e.g., "The girl is kissed by the boy") and object relatives (e.g., "The girl that the boy kissed") (e.g., Chomsky, 1977, 1986, 1965). These sentences can be described as non-canonical, since the usual word order is inverted. In passive sentences the direct object 'moves' to the subject position, in object relatives the direct object 'moves' before the subject. PD patients have difficulties processing these non canonical structures whereas performance with canonical sentences such as actives (e.g., "The boy kissed the girl") or subject relatives (e.g., "The boy who kissed the girl") is relatively preserved (Angwin, Chenery, Copland, Murdoch, & Silburn, 2006; Grossman, 1999; Grossman et al., 1992; Grossman et al., 2000, 2002; Kemmerer, 1999; McNamara, Krueger, O'Quin, Clark, & Durso, 1996; Natsopoulos et al., 1993). Similarly, HD patients have selective problems with non canonical sentences, especially when these are not plausible (e.g., "The girl that the flower waters is white"), since in this case only a correct syntactic analysis of the moved elements guarantees correct comprehension (Teichmann et al., 2005).

However, a claim about the language-specific involvement of the striatum in syntactic processing might be problematic if it is exclusively based on the study of non-canonical sentences involving syntactic movement. This is because, in addition to a more complex syntactic processing, non canonical structures involve long distance dependencies and they require more executive resources than canonical structures, such as e.g., working memory (Fiebach, Schlesewsky, Lohmann, von Cramon, & Friederici, 2005; Gibson, 1998; Just & Carpenter, 1992; King & Just, 1991 among others). Generally speaking, sentence processing requires temporary storage of word and/or phrasal information, in order to establish a link between both adjacent and non-adjacent words (Caplan & Waters, 1999; Gibson, 1998; Gordon, Hendrick, & Levine, 2002; Just & Carpenter, 1992). The association between working memory impairments and syntactic comprehension deficits has already been documented in aphasic patients (Caramazza, Basili, Koller, & Berndt, 1981; Saffran & Marin, 1975). More specifically, agrammatic patients are spared in local syntactic processes but they are impaired in syntactic relations involving non-local syntactic dependencies (Tyler, 1985). Such discrepancy has been explained in terms of a limited availability of extra-linguistic processing resources, such as working memory (Baum, 1989; Berndt, Mitchum & Haendiges, 1996; Caplan, Waters, DeDe, Michaud, & Reddy, 2007; Caramazza, Capasso, Capitani, & Miceli, 2005; Miyake, Carpenter, & Just, 1994) under the hypothesis that the number of intervening words between non-adjacent words standing in a syntactic relation increases working memory load. Indeed, the contrast between syntactic complexity per se and working memory load is often manipulated in language research by increasing the number of intervening words between the two elements of a syntactic long-distance dependency (Fiebach, Schlesewsky, & Friederici, 2001; Friedmann & Gvion, 2003; Phillips, Kazanina, & Abada, 2005; Stromswold, Caplan, Alpert, & Rauch, 1996); but see(Gordon et al., 2002; Van Dyke & McElree, 2006). However, such studies often use non-canonical sentences and thus may result in confounding effects given that even when controlling for the number of intervening words, non-canonical sentences also require the storage of the moved element in memory.

Hence, given that the striatum is involved in working memory (Gabrieli, 1995; Kensinger, Shearer, Locascio, Growdon, & Corkin, 2003; Owen, Doyon, Petrides, & Evans, 1996), it may be that this brain structure does not subserve syntactic operations as such, but that it impacts on sentence processing via its implication in verbal working memory (e.g., Grossman et al., 2000, 2002). The difficulties of patients with striatal damage in the processing of non-canonical structures involving long-distance dependencies might thus be explained by the involvement of the striatum in the transient maintenance of linguistic information. For example, in the object-relative construction "the flower that the girl waters _", the syntactic relation between the constituent "the flower" and the gap position "_" determines the semantic interpretation of "the flower" as the object of the watering action. This constituent has to be stored in working memory and it has to be subsequently retrieved when the gap position is encountered (Fiebach et al., 2001, 2005; Gibson, 1998; King & Kutas, 1995; Phillips et al., 2005, among others). A correlation between the correct interpretation of object-relatives and performance on several executive tasks involving working memory has been shown in PD patients and it has been interpreted as evidence of a direct link between sentence processing difficulty and working memory impairment (Grossman, 1999; Grossman et al., 2000, 2002; Hochstadt et al., 2006). Yet, the relation between these two behaviors could merely result from the parallel deterioration of both the syntactic system and working memory capacities in PD.

It is therefore not clear whether the syntactic impairment of patients with striatal lesions can be fully accounted for by appealing to working memory deficits, or whether it arises from a more specific deficit in syntactic processing. Previous research has not been able to settle this issue because the experimental materials did not make it possible to simultaneously manipulate syntactic relations and working memory load in a single experiment.

The present study assessed early stages of HD to test whether the striatum plays a specific role in syntactic processing, independent from its role in working memory. In order to investigate this issue, we used sentences in which we held the working memory load constant while modifying syntactic constraints, rather than using correlations with working memory scores. Furthermore, we used sentences in which the syntactic configurations could be varied while keeping a canonical word order, in order to avoid the working memory confounds which may result from the use of non-canonical sentences.

In the main experiment, referred to as the Syntax Experiment, we varied syntactic constraints while simultaneously controlling for memory load. The syntactic manipulation chosen holds the distance between two words that are linked by a syntactic relation constant, allowing us to equalize the working memory load. The sentences involved relations between a name and a pronoun. In some of the sentences, grammar allows these two constituents to refer to the same person, i.e., it allows a coreferential interpretation (e.g., "Paul smiled when he entered"), whereas in others, this is disallowed (e.g., "He smiled when Paul entered"). Importantly, while the constraints on the name-pronoun coreference vary, the linear distance in terms of number of intervening words between the name and the pronoun, which can serve as a proxy for working memory load, is the same in both sentences. The inhibition of the pronoun-to-name coreference in sentences like "He smiled when Paul entered" is due to a grammatical constraint, namely Principle C of the Binding theory (Chomsky, 1981). Binding theory comprises a set of grammatical principles regulating referential dependencies. While theories may differ as to how exactly Principle C should be formalized (Grodzinsky & Reinhart, 1993; Schlenker, 2005), they all agree on the fact that Principle C prohibits a name from co-referring with a pronoun when the pronoun is in a position of structural prominence with respect to the name, i.e., when the pronoun "c-commands" the name (e.g., when the pronoun is the subject of the main clause whereas the name is part of the subordinate clause). This phenomenon of coreference blocking under structural constraints is very robust across languages (Baker, 1991; Jelinek, 1984) and it appears early in language development (Crain & McKee, 1985; Crain & Thornton, 1998; Kazanina & Phillips, 2001).

The second experiment, referred to as the Memory Load Experiment, assessed whether the increase in verbal working memory load interferes with sentence comprehension in HD. We varied the amount of memory load by manipulating the number of words intervening between two words linked by a syntactic relation while keeping the syntactic relation between these two words constant. To do so, we used two types of relative clauses involving gender agreement between a noun and an adjective. We constructed "distant" (center-embedded) and "close" (right-branching) agreement configurations, which have a different number of intervening words between the noun and its agreeing adjective. We compared the "distant" agreement construction with the "close" agreement construction, e.g., respectively "The girl who is watching the dog is green" and "The girl is watching the dog which is green". Center-embedded relatives are claimed to involve more working memory load than right-branching structures since the noun phrase in the main clause has to be stored in memory while the subordinate clause is processed until the corresponding adjective is encountered (Gibson, 1998; Miller & Isard, 1964; Santi & Grodzinsky, 2010).

If striatal damage intervenes during the processing of syntactic structures in sentence processing, independently from working memory, HD patients should differ from controls in applying syntactic constraints on the interpretation of pronouns in Experiment 1. By contrast, if the sentence processing disorder originates primarily from a working memory disorder in HD, the patients should differ from controls when the working memory load is high. Specifically, in Experiment 1 they should have difficulties processing all long-distance dependencies between pronouns and names, and in Experiment 2 they would be expected to have poorer performance with center-embedded distant agreement sentences than with right-branching close agreement sentences.

2. Methods

2.1. Participants

Twenty-five French speaking HD patients at an early stage, classified as stage I according to the "Total Functional Capacity scale" (Shoulson, 1981) and fifteen healthy volunteers participated in this study. HD patients were recruited from the clinical follow-up program of predictive biomarkers, approved by the ethical committee at the Henri Mondor Hospital (Créteil, France). HD patients had no previous neurological or psychiatric history other than HD, and the neurological diagnosis was genetically confirmed (CAG repeats >35). Only fifteen patients could be included in the analyses, since the remaining 10 demonstrated a severe deficit in attentional control sentences. These fifteen patients were matched to the fifteen healthy controls. Healthy controls had no neurological or psychiatric disorders and were matched to HD patients according to their age and educational level (all $Fs<1$). Medication varied across patients (6 without medications and, 7 having antidepressants, 4 neuroleptics, 3 thymoregulators, 4 benzodiazepines and 4 others). All participants gave informed consent. Demographic data is summarized in Table 1.

2.2. General assessment

All patients were evaluated using the Unified Huntington's Disease Rating Scale (UHDRS; Huntington_Study_Group, 1996) and the Mattis Dementia Rating Scale (MDRS; Mattis, 1976). The UHDRS comprises the evaluation of functional abilities (Total Functional Capacity; TFC), of motor functioning (UHDRS motor part) and of cognitive executive functions such as Literal Fluency, the Stroop test and the Digit Symbol Code (UHDRS cognitive part). The digit span task from the MDRS (forward and backward) was singled out in addition to the French version of the Hopkins Verbal Learning Test (Rieu, Bachoud-Levi, Laurent, Jurion, & Dalla Barba, 2006) to assess memory capacities. General assessment is summarized in Table 2.

Table 1
Demographic data of HD patients and controls (means ± standard deviations).

	HD	Controls
N	15	15
Sex	10F/5M	14F/1M
Age (years)	43.7 ± 9.0	47.7 ± 10.2
Educational level (years)	12.3 ± 2.6	13.13 ± 2.2
Laterality	15R	13R/2L
Evolution duration (years)	6.5 ± 3.3	–
CAG repeat length	44 ± 2.7	–

Table 2
Clinical performance of HD patients (mean values ± standard deviations).

	HD	Published norms
Total functional capacity	12.0 ± 0.9	13
UHDRS motor score	17.9 ± 14.9	–
Stroop color/word	32.7 ± 10.3	> 35[a]
Letter fluency[b]	48.7 ± 26.4	> 56[c]
Symbol digit code	31.7 ± 13.4	37[d]
MDRS[b]	133.3 ± 8.9	> 136 [e]
Forward span	3.87 ± 0.35	4 [e]
Backward span	3.13 ± 0.91	4 [e]
Hopkins verbal learning test	21.8 ± 6,3	36.3 ± 0.37[f]
MADRS	7067 ± 7, 36	=

[a] Golden (1978);
[b] Letter fluency used the letter PRV in 2 min;
[c] Cardebat, Doyon, Puel, Goulet, and Joanette (1990);
[d] Wechsler (1981);
[e] Mattis (1976));
[f] Rieu et al. (2006).

General intellectual functions, consistently with their Stage I of Huntington's disease, were slightly impaired in these patients (MDRS). Executive and memory dysfunction were mild. Patients were not depressed regarding to their score at the Montgomery and Asberg Depression Scale (MADRS).

2.3. Experimental design

Both experiments used a sentence-picture matching-task because it has been shown to boost syntactic processing by imposing participants to fully comprehend the sentence before responding (Crain, Ni, & Shankweiler, 2001). In this task, a sentence is provided auditorily and the participant is presented several pictures among which he has to choose the one whose content matches the one of the sentence. The simplicity of the experimental procedure explains its large use in various populations including healthy adults (Meltzer, McArdle, Schafer, & Braun, 2010), healthy children (Smith, Macaruso, Shankweiler, & Crain, 1989), children with Williams syndrome (Perovic & Wexler, 2010), aphasic patients (Lukatela, Shankweiler, & Crain, 1995). However, because attentional and memory disorders might hamper the results, we adapted the task, as we had also done in previous studies of syntactic impairment in Huntington's disease patients (Teichmann et al., 2005, 2008). Rather than exposing patients to multiple pictures, we limited working memory load and attention demands by only showing them one sentence and one picture, expecting a YES or a NO response depending on whether the sentence correctly matched the picture.

2.4. Syntax Experiment

In this experiment we varied the syntactic configuration of the name-pronoun relation while holding the working memory load constant. In the first type of sentence, the name c-commands and linearly precedes the pronoun (AmbN1). These sentences are ambiguous, since both a coreferential and a non-coreferential interpretation of the pronoun and the name are grammatical: 'He' and 'Paul' can refer to the same person or not (e.g., "Paul a souri quand il est entré"; "*Paul smiled when he entered*"). In the second type of sentence, referred to as "Principle C sentences" (PC), the pronoun c-commands and linearly precedes the name, thus blocking a coreferential interpretation (e.g., "Il a souri quand Paul est entré"; "*He smiled when Paul entered*"). In both sentence types the number of words between the name and the pronoun was kept exactly the same in order to equalize the memory load. A third type of sentence was used to verify that performance on the two previous sentence types specifically depends on the processing of the required syntactic relation (c-command) rather than on the linear position of the pronoun. Just as in the second type of sentence, the pronoun linearly precedes the name (AmbP1) but in this case coreference is allowed because the pronoun belongs to the subordinate clause, and as a result it no longer c-commands the name (e.g., "Quand il est entré Paul a souri"; "*When he entered, Paul smiled*"). Each sentence was matched with 3 pictures.

The pictures represented one person designated as "Paul" by the name written on his t-shirt and another one whose name was not specified (e.g., Picture 1: "Paul" smiling and entering, Picture 2: "Paul" smiling and the other person entering). Each sentence was presented once with a picture depicting a coreferential interpretation (e.g., the same person smiling and entering) and once with a picture depicting a non-coreferential interpretation of the sentences (e.g., one person smiling and the other one entering). In addition, to verify that the participants were able to correctly execute the task (in terms of attention and response bias), each sentence was paired with a picture in which "Paul" is misidentified (e.g., the sentence states "Paul entered…" but the picture shows the other person entering). These latter sentence-picture pairs are referred to as the "attentional control condition". In contrast to the other conditions, which specifically test linguistic knowledge, in the attentional condition all pictures mismatched with the sentences and thus required "NO" answers. "YES" responses in this condition could indicate either a response bias to respond "YES", or alternatively that the participant is not paying attention to the picture. The attentional condition was thus designed to reduce possible language-independent artifacts of participants' responses. Materials are summarized in Fig. 1.

2.5. Memory load experiment

Here we manipulated the memory load using relative structures with distant agreement (e.g., "La fille qui regarde le chien est verte"; "*the girl who is watching the dog is green*") or close agreement (e.g., "La fille regarde le chien qui est vert"; "*the girl is watching the dog which is green*"). We use the fact that gender is phonologically marked in French. Each sentence was matched once with a picture which correctly depicts it (e.g., a green dog) and once with a picture which does not (e.g., a green girl). For example, the participant who was presented with a picture depicting a girl watching a green dog and to the sentence "the girl is watching the dog which is green", was supposed to say YES. On the contrary, if the picture was depicting a green girl watching a (white) dog, the expected answer was NO.

Moreover, in order to detect a potential response strategy simply based on matching the color of the characters in the picture to the gender of the adjective in the sentence, we used two types of ungrammatical control sentences. The ungrammaticality of these sentences was due to the fact that the phonologically marked gender agreement was incorrect (e.g., "La fille$_{[feminine]}$ qui regarde le chien est vert$_{[masculine]}$"; "*the girl*$_{[feminine]}$ *who is watching the dog is green*$_{[masculine]}$" and "La fille regarde le chien$_{[masculine]}$ qui est verte$_{[feminine]}$"; "*the girl is watching the dog*$_{[masculine]}$ *which is green*$_{[feminine]}$)". In the former sentence, the constituent "la fille" requires the feminine gender marker "verte"; in the latter sentence, the constituent "le chien" requires the masculine gender marker "vert". Pairing these two ungrammatical sentences with the two types of pictures yields four sentence-picture patterns, which we grouped in two types of pairs according to congruency (see Fig. 2). In congruent pairs, the gender on the adjective (e.g., "verte") matches the gender of the noun corresponding to the green-colored character in the picture (e.g., "la fille"). In non-congruent pairs, the gender on the adjective (e.g., "verte") does not match the gender of the noun corresponding to the green-colored character in the picture (e.g., "le chien"). In ungrammatical sentences, there is by definition no correct answer and the expected answer reflects whether or not the subject uses a strategy based on the congruence between the gender of the colored character and the gender of the adjective. Nevertheless, if participants refer only to congruency between the character and the gender, they should respond YES to congruent pairs and NO to incongruent pairs regardless of the syntax of the sentence.

3. Materials

The Syntax Experiment comprised 6 ambiguous sentences with the name in the first position in the main clause (AmbN1), 6 ambiguous sentences with the pronoun in the first position in the subordinate clause (AmbP1) and 6 PC sentences (PC). This resulted in a total of 18 sentences. Each sentence was matched with three pictures, depicting, respectively, the coreferential interpretation, the non-coreferential interpretation and the attentional control where the characters are not performing the action depicted in the picture. This yielded a total of $3 \times 18 = 54$ sentence-picture pairs (see Fig. 1).

The Memory Load Experiment comprised 6 distant agreement relatives, 6 close agreement relatives, 6 ungrammatical distant agreement relatives and 6 ungrammatical close agreement relatives. This resulted in a total of 24 sentences. Each sentence was paired with two pictures, which contained two characters each, yielding a total of $24 \times 2 = 48$ sentence-picture pairs. For grammatical sentences, one picture matched the meaning of the sentence and the other did not. The materials are summarized in Fig. 2.

3.1. Procedure and apparatus

The sentence-picture pairs of the syntax and the Memory load experiments were mixed together and presented to each patient in a randomized order. Each stimulus trial consisted of the presentation of a fixation cross (+) in the middle of a computer screen for 1000 ms, followed by the auditory test sentence that was heard through headphones. The picture was presented immediately after the last word of the sentence and filled the whole computer screen. Participants were instructed to decide whether the picture correctly illustrated the sentence, and to do so as accurately and as quickly as possible. They were told to press the button corresponding to their dominant hand if they thought the answer was YES and the button corresponding to their non-dominant hand if they thought the answer was NO. Reaction times were measured from the moment the picture appeared. Each picture was shown on the computer screen for 5 s. All responses occurring after this delay were excluded from the analyses. A new trial was initiated 1000 ms

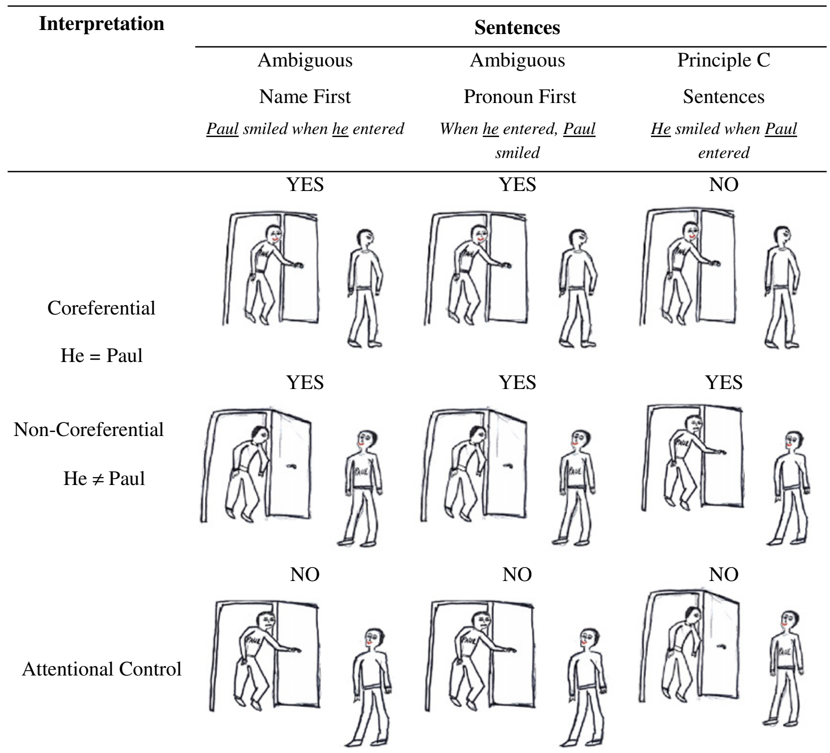

Fig. 1. Sentence-picture pairs in Syntax Experiment: expected answer for interpretation type.

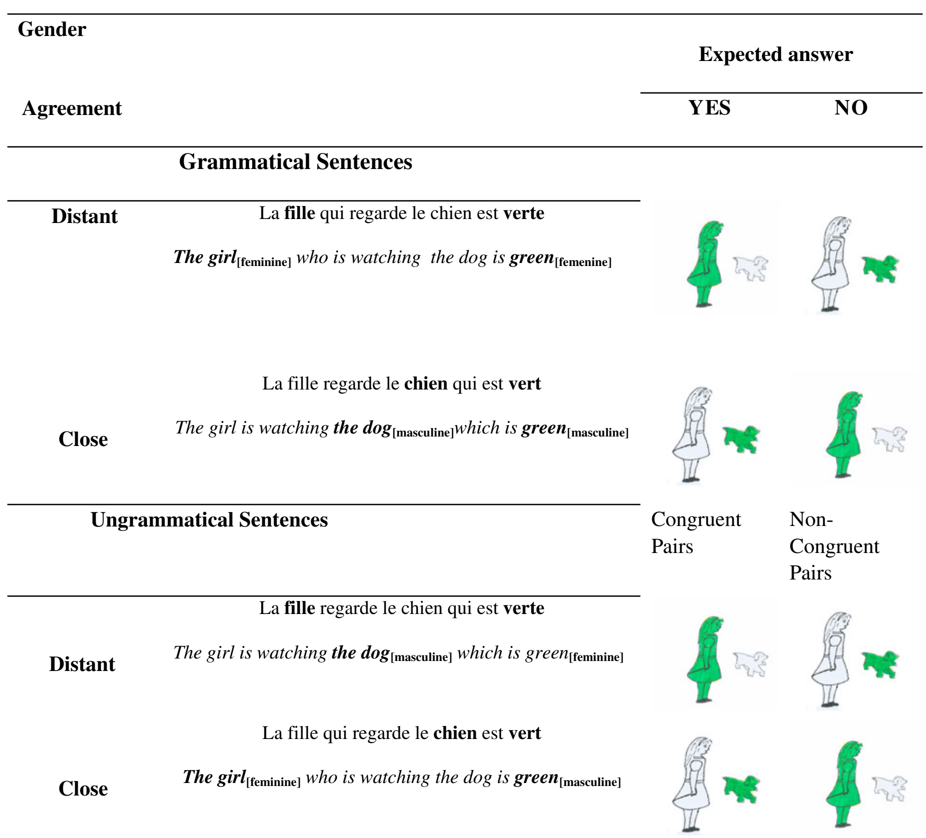

Fig. 2. Sentence-picture matching for grammatical and ungrammatical sentences in the Memory load Experiment: expected answers on gender agreement. *The expected answer in grammatical sentences is straight forward and is based or the correctness of the sentence-picture matching. Participants should answer yes in congruent pairs (left column) and no in non-congruent pairs (right columns).*

after the response. The total duration of the experimental session was approximately 20 min. In order to familiarize participants with the task, six training trials were provided using three sentence-picture pairs, similar to the pairs in the Syntax Experiment, and three sentence-picture pairs, similar to the pairs in the memory load experiment. We introduced the character referred to by the name "Paul", to ensure that the participant recognized that somebody was called Paul and was recognizable by his name on his T-shirt. Participants were then encouraged to identify the character marked as "Paul" on the pictures in order to make rapid and correct decisions on the sentences. All sentences were recorded by a native French male speaker and digitized for binaural presentation over headphones using Cool Edit software. The experiment was administered on a Dell laptop computer using E-Prime experimental software.

4. Results

Analyses of variance (ANOVAs) were conducted by participants (F_1) and by items (F_2). Accuracy data will be provided in terms of percentage of correct responses; d-prime could not be calculated given the number of trials. First, we calculated mean performances on the attentional control condition of the Syntax Experiment. HD patients whose accuracy deviated by more than two standard deviations from the controls were excluded from the analyses. This yielded the exclusion of 10 out of the 25 patients who were initially assessed. The performance of the remaining 15 patients in the attentional control condition was similar to that of controls (correct responses: controls 92.8% ± 10.3; HD patients 88.3% ± 16.3; $F_1(1, 28)=1.70$, $p>0.1$; $F_2(1, 15)=2.82$, $p>0.1$). Statistical analyses were conducted separately for the Syntax Experiment and the Memory Load Experiment. Mean reaction times (RT) and standard deviations were calculated for each participant. Trials on which the RT deviated by more than two standard deviations from the mean values for each condition were excluded from the analyses. This yielded the exclusion of 2.9% of the data for HD patients and 1.6% for controls.

4.1. Syntax Experiment

We performed ANOVA's with "YES answers" as the dependent variable and with three independent variables: "group" (HD, controls), "sentence type" (PC sentences (PC), ambiguous name first (AmbN1), ambiguous sentences pronoun first (AmbP1) and "interpretation type" (coreferential, non-coreferential, attentional control). HD patients produced more YES answers (60.1% ± 37) than controls (47.0% ± 32; $F_1(1, 28)=11.41$, $p=0.002$; $F_2(1, 45)=47.05$, $p<0.001$). We found a sentence type effect in the analysis by participants (PC 43.5% ± 35, AmbP1 53.3% ± 39, AmbN1 50.4% ± 38; $F_1(2, 56)=10.17$, $p<0.001$) and approaching significance in the analysis by items ($F_2(2, 45)=3.80$, $p=0.08$) and an interpretation type effect (coreferential 72.0% ± 33, non-coreferential 65.7% ± 25, attentional control 9.5% ± 14; $F_1(2, 56)=222.38$, $p<0.001$; $F_2(2, 45)=133.32$, $p<0.001$). There was a sentence type *x* interpretation type interaction ($F_1(4, 112)=49.92$, $p<0.001$; $F_2(4, 45)=16.02$, $p<0.001$) and a triple group *x* sentence type *x* interpretation type interaction ($F_1(4, 112)=12{,}24$, $p<0.001$; $F_2(4, 45)=12.34$, $p<0.001$). Results are summarized in Fig. 3. Restricted analyses showed that for ambiguous sentences, coreferential interpretations were more frequent than non-coreferential interpretations in both controls ($F_1(1, 29)=49.29$, $p<0.001$; $F_2(1, 11)=21.46$, $p=0.001$) and HD patients ($F_1(1, 29)=28.20$, $p<0.001$; $F_2(1, 11)=10.80$, $p=0.007$). For both types of ambiguous sentences (AmbN1 and AmbP1) HD patients like controls accepted more frequently the sentence-picture pairs giving a coreferential interpretation than the pairs giving a non-coreferential one (AmbP1sentences controls: coreferential 93.1% ± 9, non-coreferential 62.7% ± 21; HD patients: coreferential 85.6% ± 25, non-coreferential 63.3% ± 26, and AmbN1sentences: controls: coreferential 89.3% ± 19, non-coreferential 52.4% ± 18; HD patients coreferential 84.8% ± 26, non-coreferential 58.7% ± 30). There was no group *x* interpretation type interaction either for AmbP1 ($F_1(1, 28)=1.14$, $p>0.1$; $F_2(1, 10)=1.32$, $p>0.1$) or for AmbN1 ($F_1(1, 28)=1.02$, $p>0.1$; $F_2(1, 10)=1.23$, $p>0.1$). Conversely, for PC, controls preferred the non-coreferential interpretation ($F_1(1, 14)=105.38$, $p<0.001$; $F_2(1, 10)=54.14$, $p<0.001$) whereas there this preference was not observed in HD patients ($F_1(1, 14)=1.15$, $p>0.1$; $F_2<1$).

We performed similar ANOVAs with reaction times (RTs) as the dependent variable. RTs for YES answers (accepting the sentence picture pairs) were analysed. Responses were faster for controls than for HD patients (controls 2453 ms ± 531; HD 2826 ms ± 616; $F_1(1, 28)=4.81$, $p=0.037$, $F_2(1, 45)=81.68$, $p<0.001$). There was a sentence type effect (PC: 2792 ms ± 610, AmbN1 2631 ms ± 615, AmbN1 2497 ms ± 554; $F_1(2, 56)=17.73$, $p<0.001$, $F_2(2, 45)=6.42$, $p=0.004$) and an interpretation type effect (coreferential 2539ms ± 667, non-coreferential 2687ms ± 564, attentional control 2693ms ± 568) in the analysis by participants ($F_1(2, 56)=7.83$, $p=0.001$) and approaching significance in the analysis by items ($F_2(2, 45)=2.83$, $p=0.069$). There was a sentence type *x* interpretation type interaction ($F_1(4, 112)=7.66$, $p<0.001$; $F_2(4, 45)=3.51$, $p=0.014$). However, this profile did not differ between groups (no triple group × sentence type × interpretation type interaction ($F_1(4, 112)=1{,}17$, $p>0.1$; $F_2(4, 45)=1.20$, $p>0.1$). Despite the fact that HD patients differed from controls in the percentage of YES answers for ambiguous and PC sentences, they had the same profile as controls for RTs with these answers. RTs were slower to PC sentences than to AmbN1 sentences in both controls ($F_1(1, 14)=13.15$, $p=0.003$; $F_2(1, 34)=9.33$, $p=0.004$) and HD ($F_1(1, 14)=10.03$, $p=0.007$; $F_2(1, 34)=12.02$, $p=0.001$). Likewise, RTs to PC items were slower than to AmbP1 (controls: $F_1(1, 14)=3.68$, $p=0.07$; $F_2(1, 34)=3.02$, $p=0.09$; HD: $F_1(1, 14)=5.46$, $p=0.04$; $F_2(1, 34)=6.91$, $p=0.01$). There was no group *x* sentence type interaction for the PC vs. AmbN1 contrast ($F_1<1$, $F_2<1$ and $p>0.1$) nor for the PC vs. AmbP1 contrast ($F_1<1$ and $p>0.1$, $F_2(1, 34)=1.46$, $p>0.1$). Since the analyses for 'YES' answers included not only RTs with correct answers (accepting coreferential interpretation) for ambiguous sentences but also false positive incorrect answers (accepting coreferential interpretation) for PC sentences, we ran supplementary ANOVAs comparing RTs for correct answers in both types of sentences. We compared RTs for 'NO' answers to the coreferential interpretation in ambiguous (AmbN1 and AmbN1) and PC sentences. PC sentences were faster than Ambiguous in both controls (Controls: PC 2731 ms ± 113, Ambiguous 3642 ms ± 384) and HD patients (HD: PC 3047 ms ± 244, Ambiguous 3806 ms ± 229), yielding a sentence type effect $F(1, 5)=7.71$, $p=0.039$). There was no group effect $F_1<1$) and no sentence type *x* group interaction ($F_1<1$).

4.2. Memory load Experiment

ANOVAs were carried out on both performance and RTs as the dependent variables, first in grammatical sentences then in ungrammatical sentences. The independent variables were "group" (HD, controls) and "agreement type" (distant agreement sentences: DA; close agreement sentences: CA).

In grammatical sentences, performance was similar in controls (96.3% correct ± 8) and HD patients (88.8% correct ± 17) in the analysis by participants ($F_1(1, 28)=2.72$, $p>0.1$) but not in the analysis by items ($F_2(1, 22)=18.44$, $p<0.001$). Performance was similar with both agreement types (DA: 91.2% corrects ± 15, CA: 94.0% correct ± 12; $F_1(1, 28)=2.68$, $p>0.1$, $F_2(1, 22)=2.69$, $p>0.1$) without a group *x* sentence type interaction ($F_1<1$; $F_2(1, 22)=1.05$, $p>0.1$). Results are summarized in Fig. 4. RTs were faster in controls (1631 ms ± 69) than in HD patients (2158 ms ± 108; $F_1(1, 28)=9.39$, $p=0.005$, $F_2(1, 22)=75.53$,

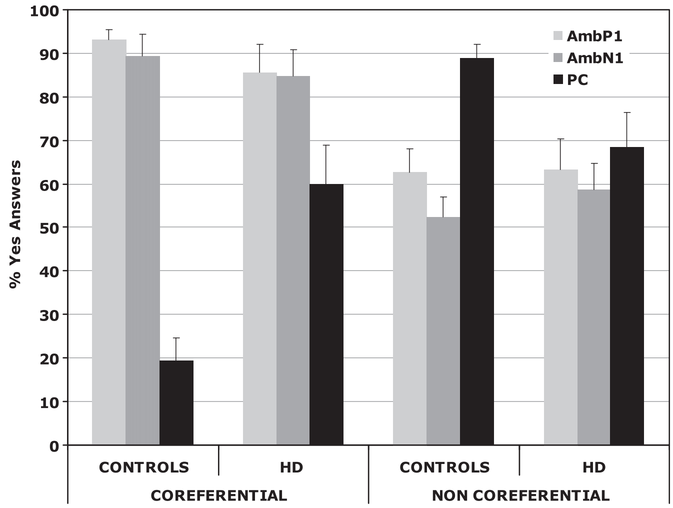

Fig. 3. Percentage of Yes answers (Mean+Standard Error) in Experiment 1 (Syntax Experiment) as a function of interpretation type for each of the three sentence types in both HD patients and their controls.

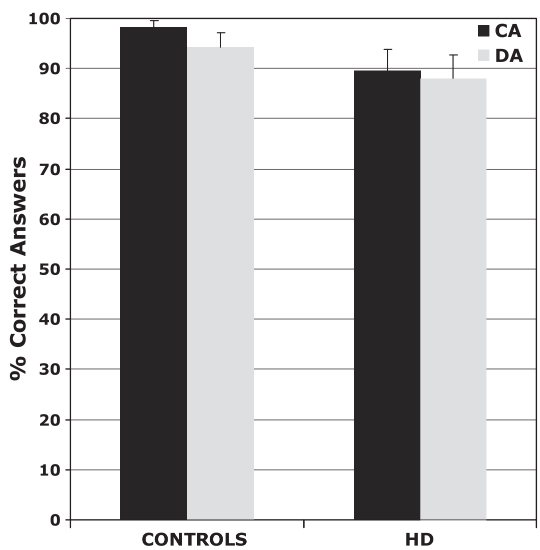

Fig. 4. Percentage of correct responses (Mean+Standard Error) with close agreement (CA) and distant agreement sentences (DA) in grammatical sentences in controls and HD patients.

$p<0.001$). They were similar for both agreement types (DA 1861 ms ± 577, CA 1928 ms ± 549; $F_1(1, 28)=1.05$, $p>0.1$, $F_2<1$) without a group *x* agreement type interaction ($F_1(1, 28)=1.18$, $p>0.1$, $F_2(1, 22)=2.37$, $p>0.1$).

In ungrammatical sentences, performance ("YES" answers) was used as the dependent variable; the independent variables were "group" (HD, controls) and "sentence-picture type" (congruent gender agreement, non congruent gender agreement). Performance was similar in controls (33.2% ± 27) and HD patients (43.4% ± 28) in the analysis by participants ($F_1(1, 28)=1.79$, $p>0.1$) but not in the analysis by items ($F_2(1,22)=17.52$, $p<0.001$). Performance was similar with both sentence-picture types (congruent gender agreement 36.3% ± 27, non-congruent gender agreement 40.0% ± 29; $F_1<1$, $F_2<1$) without a group *x* sentence-picture type interaction ($F_1<1$, $F_2<1$). Results are summarized in Fig. 5. RTs with ungrammatical sentences showed that controls were faster than patients (Controls: 2356 ms ± 541; HD: 2602 ms ± 438; $F_1(1, 14)=14.09$, $p=0.002$; $F_2(1, 11)=44.14$, $p<0.001$). Congruency did not influence RT in controls ($F_1<1$, $F_2<1$) or in HD ($F_1<1$; $F_2(1, 11)=2.99$, $p>0.1$). There was no group *x* sentence-picture type interaction ($F_1<1$, $F_2<1$).

5. Discussion

In this study, we investigated the role of the striatum in sentence processing through the study of patients at early stages of HD. First, we explored whether striatal damage impairs sentence comprehension independently from working memory. We tested this by manipulating syntactic properties related to name-pronoun relations while equalizing memory load. Our results show that in contrast to controls, HD patients do not correctly block the coreferential interpretation of the name and the pronoun in sentences, which are constrained syntactically by principle C. Second, we varied the memory load by contrasting the processing of noun-adjective gender agreement in center-embedded and right-branching relative clauses. In this case HD patients performed similarly to controls. Finally, using ungrammatical sentences we found that patients do not follow simple gender matching strategies, suggesting that they apply syntactic analyses like controls. Altogether, these results suggest that the patients' difficulties in sentence processing cannot be reduced to working memory difficulties. This indicates a role of the striatum in syntactic processing which is independent from verbal working memory.

In particular, the Syntax Experiment reveals deficits for the processing of principle C sentences. Since these sentences involve the same working memory load — in terms of number of intervening words between the pronoun and the name as ambiguous sentences (Tyler, 1985) the deficit cannot be explained by a working memory deficit. In agreement with previous psycholinguistic research (Gordon & Hendrick, 1997), healthy individuals showed a preference for a coreferential interpretation of ambiguous sentences, but crucially this preference radically drops for sentences, where Principle C blocks coreference. In contrast, HD patients did not block this preference while processing sentences constrained by Principle C, while showing a comparable coreferential interpretation for ambiguous sentences. They accepted the coreferential interpretation in about 60% of Principle C sentences

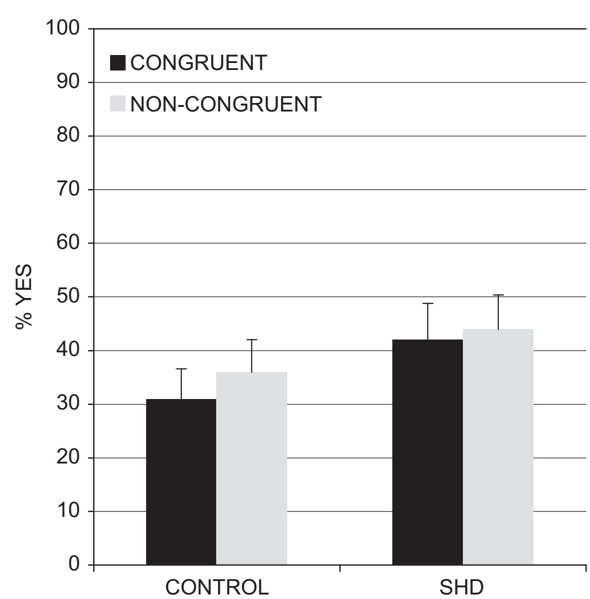

Fig. 5. The Memory load Experiment (non grammatical sentences): Percentage of "YES" answers (Mean +Standard Error) with congruent and non-congruent gender agreement pairs.

and accepted the non-coreferential interpretation in a fairly similar 70% of cases. On the one hand HD patients accepted sentence-picture pairs with a coreferential interpretation more readily, and on the other hand they had lower acceptance than controls of those pairs giving a non-coreferential one. This shows that they do not have a mere bias for YES answers, nor a bias to accept any sentence-picture pair; they just prefer the coreferential interpretation even in principle C sentences.

The fact that HD patients preferred the coreferential interpretation in ambiguous sentences and even in Principle C contexts also suggests that they memorize the pronoun (or the name) until the referring name (or pronoun) is encountered. This in itself rules out a working memory deficit as the source of the observed syntactic deficit. Evidence from healthy individuals (Kazanina, Lau, Lieberman, Yoshida, & Phillips, 2007) shows that the presence of a pronoun without a prior antecedent initiates a search for potential antecedents: participants in a self-paced reading task slowed down when encountering a potential antecedent that did not qualify as antecedent because of morphological restrictions (gender mismatch) suggesting that they predicted the occurrence of a potential antecedent. By contrast, in sentences in which the pronoun c-commands a potential antecedent, healthy adults do not slow down reading when encountering this potential antecedent does not match the gender of the pronoun, suggesting that the search for antecedents is blocked where Principle C would exclude coreference (Kazanina et al., 2007).

An additional argument for spared memory capacities with respect to sentence processing is provided by HD patients' normal performance with gender agreement in relative clauses, independently from the number of words separating the noun and the agreeing adjective (center-embedded vs. right-branching). The fact that they were accurate in the comprehension of the main clause suggests that they were able to keep in memory the information about the noun phrase ('*La fille*'—'*The girl*') while processing the subordinate clause ('*qui regarde le chien*'—'*that is watching the dog*') until the information about the gender appeared in the main clause ('*est verte*'—'*is green*'). Their correct performance with both center-embedded and right-branching relatives apparently contrasts with findings with PD patients, who have been reported to demonstrate poorer performance with center-embedded relatives (Hochstadt, 2009). In addition, HD patients performed like controls in answering to ungrammatical sentences: they respond with a similar number of YES responses in congruent and non-congruent pairs. This suggests that they do not use a simple color-gender strategy and rather rely on more or less correct syntactic analysis for interpreting grammatical sentences. This result contrasts with their diverging performance in Principle C sentences.

Altogether, our results show that HD patients are impaired with some syntactic processing, and that this impairment is independent from the working memory capacities required for sentence comprehension. This syntactic deficit however does not encompass all aspects of syntax, thus contradicting proposals which attribute to the striatum a general function in the application of linguistic rules (Ullman, 2001, 2006).

Our findings also shed some light on the nature of working memory capacities used during sentence processing. In line with studies showing that the striatum is involved in working memory (consistently with numerous studies, e.g., Gabrieli, 1995; Kensinger et al., 2003; Owen et al., 1996), our HD patients had deficits on general working memory tests such as the forward and backward Span and the Hopkins Verbal Learning Test. Yet, according to Caplan and Waters (1999) such standard tasks tap working memory components, which are distinct from working memory resources used during syntactic processing. This distinction between general purpose working memory and working memory tied to syntactic processing is consistent with previous results obtained in PD patients (Caplan & Waters, 1999). It is also consistent with the finding that nonfluent agrammatic patients differ from nonfluent aphasics without agrammatism with respect to their syntactic abilities, in spite of the fact that their memory spans were similar (Martin, 1987). A single syntactic deficit is unlikely to explain the variability of profiles of comprehension in aphasic patients (Berndt et al., 1996; Caplan et al., 2007; Caramazza et al., 2005). However, limitations of general purpose working memory and executive functioning due to striatal lesions may affect the patients' sentence comprehension. Indeed, such deficits caused the exclusion of 10 patients from the analyses out of the 25 HD patients tested in our study, because they failed the attentional condition. Yet importantly, when this effect was controlled for, a syntactic deficit was still present in the remaining participants.

One point to highlight for the interpretation of the results is that both controls and HD patients prefer coreference in the processing of ambiguous sentences. In our study, such a preference is reflected through the higher acceptance of coreferential pairs, as well as by the lower acceptance of non-coreferential ones. The general preference for a coreferential interpretation is consistent with results from previous psycholinguistic research on healthy individuals. Indeed, studies using different tasks but sentences that are syntactically comparable to the sentences used in the present study have shown that coreference is preferred (at about a rate of 90%) for ambiguous sentences such as "*before she began to sing, Susan stood up*" and "*Susan began to sing when she stood up*" where the pronoun does not c-command the name, but the acceptance of coreference drops to about 5% for sentences where Principle C blocks coreference (Gordon & Hendrick, 1997). The present study is comparable to previous ones with respect to the fact that healthy participants reject a coreferential interpretation for sentences in which coreference is ruled out by Principle C. However, the acceptance of coreference in these sentences, in around 20% of cases, is relatively high compared to previous studies, reported in around 5–10% of cases. This greater preference for coreference is also observed in the ambiguous sentences with a higher acceptance of coreference for ambiguous sentences as compared to previous studies: 90% in our study vs. 80% in Crain and Thornton (1998). This contrast can be explained by the differences in the respective paradigms. In the Crain and Thornton study, the character referred to by the pronoun had already been introduced before running the experiment; this made the task of connecting the pronoun to this entity external to the sentence easier. Conversely, in our experiment, only the character "Paul" was introduced to the participants before the experiment. The other character referred to by the pronoun (e.g., "He") was never introduced, nor given a specific name or entity; its identity could therefore only be pragmatically inferred in the context of the experiment by an exclusion criteria when a coreferential interpretation is not possible. Since a pronoun without prior antecedent initiates a search, the higher preference for selecting as its referent the character referred to with the proper name in the sentence may be explained by the need to close this search. This explanation is consistent with the overall tendency to prefer coreference in both ambiguous and principle C sentences. In other words, the differences between previous results and ours can be explained by the baseline 'default' preference for coreference, which is slightly higher in our study as compared to previous ones, it being harder to pragmatically assign an external reference to "he". The 'default' preference when encountering a pronoun and a name is to interpret them as being coreferential: principle C interferes by reversing this tendency and triggering a rejection of coreference. These results provide novel behavioral evidence of the effects of Principle C by using a different task design and by extending results to French.

The effect of a default preference for a given interpretation in sentence processing can be referred to as dominance (Rodd, Longe, Randall, & Tyler, 2010). Previous literature has outlined the relevance of similar frequency and/or expectation effects: when faced with syntactically and semantically ambiguous information, individuals are more likely to interpret sentences according to a dominant or preferred alternative, which is determined by the frequency of occurrence (Hale, 2001; Levy, 2008; MacDonald, Pearlmutter, & Seidenberg, 1994; McRae, Spivey-Knowlton, & Tanenhaus, 1998). The notion of dominance therefore implies the existence of a continuum ranging from more to less preferred interpretations. In the case of our study, both YES and NO responses would have been equally correct for ambiguous sentences. It appears however that control participants preferred the coreferential interpretation in around 80% of the times. Thus interpreting these results in terms of a "dominance" perspective seems particularly suited. On the contrary, because of the syntactic constraint, in Principle C sentences one might argue that there is no such thing as a "preferred interpretation": only a single correct answer is possible. If this were the case, the decision process invoked in performing the task would be different in the two conditions. Control participants however reject the coreference only in 80% responses in principle C sentences, indicating a comparable decision process in both conditions. The longer reaction times found in Principle C sentences, compared to ambiguous ones may reflect this additional computation to reject a strongly prevailing coreferential dominant interpretation.

The deficit of HD patients deficit could therefore derive from an inability to switch or inhibit from canonical/frequent operations to less frequent procedures (see also Hochstadt, 2009; Longworth et al., 2005). Striatal damage may reduce inhibition of the most frequent syntactic operations leading to the persistence of the most frequent rule by default (Teichmann et al., 2008, 2005). In fact, in spite of their low performance in Principle C sentences, when the dominant coreferential reading needed to be rejected, HD patients and controls showed the same increase in RT as compared to ambiguous sentences. Such discrepancy speaks against a mere difficulty of principle C sentences. If Principle C sentences were simply more difficult to process, RTs for those sentences should show greater differences between controls and HD patients, mirroring the performance results. In contrast, this suggests that, like controls, patients detect the occurrence of the syntactic constraint, even if they are unable to correctly apply it to the sentence context (that is, by rejecting a coreferential interpretation). Their flawless performance with the other syntactic conditions of this experiment suggests that this deficit in correctly applying syntactic rules only arises when the sentential context requires applying infrequent procedures. This results in the application of the default procedure regardless of the context. This behaviour may reflect impairment for correctly applying the rule to the appropriate context rather than a loss of the rule knowledge. It further suggests that the striatum holds a general function in cognition in adapting the changing environment by selecting the behavior which is more adapted to the context (Franck, Loughry, & O'Reilly, 2001; Garcia-Munoz, Carrillo-Reid, & Arbuthnott, 2010; Graybiel, 2008; Hazy, Frank, & O'Reilly, 2007; Marsden & Obeso, 1994; Monchi, Petrides, Petre, Worsley, & Dagher, 2001; Redgrave, Prescott, & Gurney, 1999; Tricomi, Balleine, & O'Doherty, 2009; Yin & Knowlton, 2006; Yin et al., 2009).

The inability to apply infrequent procedures is in line with previous results detecting an association between striatal lesions and deficits for processing non-canonical sentences. The canonical word order is the most frequent way in which individuals produce sentences, and the order in which they expect a sentence input. Previous results in HD patients with a similar sentence-picture matching task agree with the hypothesis that the deficit for processing non-canonical sentences can also be explained in terms of applying the more frequent rule, irrespectively from the context (Teichmann et al., 2008). In a lexical decision task for words which were semantically related to idioms, HD patients, showed priming for words that were semantically related to idioms even when they were presented in the passive voice ('Paul was kicked by the bucket' priming "dead"), in which the idiomatic reading is lost for control subjects. The results suggested that HD patients may actually treat non-canonical sentences according to default canonical word order ("Paul kicked the bucket") (Teichmann et al., 2008). Similarly, in a study with PD patients, when eye-movements were recorded in a subgroup of PD patients showing more pronounced deficit for sentence comprehension, they had preferential looks to the distracter picture representing the first noun phrase of passive sentences as being the subject of the performing action (Hochstadt, 2009). This suggests that they processed passive sentences as if they were actives. HD patients may assign thematic roles according to the canonical word order, which would result in a deficit in processing non-canonical sentences. The same explanation is consistent with the deficits described in HD patients in verbal morphology (Teichmann et al., 2005). The French verbal system is richer than the English one since it involves two types of conjugation rules. When tested with verbal morphology, French HD patients showed a dissociation within the regular verbs: they applied the most frequent conjugation rule of French when they were asked to conjugate non-verbs that require a less frequent sub-rule. Such over-regularizations were also reported in HD and PD patients who were tested on the English past tense, producing forms like "dig-ed" instead of "dug" (Ullman et al., 1997).

Finally, it is worth mentioning that this hypothesis may also be expressed as the inability to switch from canonical/frequent operations to less frequent procedures (see also Hochstadt, 2009). Striatal damage may reduce inhibition of the most frequent syntactic operations leading to the persistence of the most frequent rule by default (Teichmann et al., 2008, 2005). The overall results could be interpreted as a difficulty in patients with striatal lesion to inhibit competing alternatives in language (Longworth et al., 2005), as well as to learn new regularities (Cools, Clark, Owen, & Robbins, 2002; Lawrence et al., 1998). Longworth et al. (2005) proposed that the striatum suppresses lexically appropriate alternatives when trying to inflect novel verbs (e.g., 'bang-ed' instead of 'slamm-ed'). However, in contrast to the rule/lexicon dichotomy theory (Ullman et al., 1997), they did not find that regular and novel verbs were more impaired than irregular verbs in patients with striatal dysfunction. Using a priming task, they showed that unlike control subjects PD patients displayed priming for similar sounding word pairs (e.g., captive – captain) suggesting that striatal damage results in difficulty inhibiting inappropriate lexical items, beyond verb conjugation. In semantics, Copland (2003) provided evidence that patients with striatal dysfunction fail to suppress the more infrequent meaning association between targets and primes (bank-river vs. bank-money), resulting in similar priming effects for both types of prime-target pairs. In a verb-noun production task, (Crescentini, Shallice, & Macaluso, 2010) showed in healthy participants that the striatum allowed the inhibition of the competing noun alternative when producing verbs. These results are in line with our previous studies. Indeed, in HD, patients processed passives like actives in artificially passivated idioms thus leading to impaired comprehension (Teichmann et al., 2008, 2005). Similarly, coreference is not inhibited as it should be in Principle C sentences. Finally, the main conjugation rule is applied even in verbs that should respond to less frequent rules (for instance, in French, they apply the main rule in –er instead of the less frequent rule in –ir) (Teichmann et al., 2005) and in English, in irregular verbs thus producing over regularization (e.g., runed instead of ran) (Ullman et al., 1997). Such results suggest that the striatum may hold a general function in inhibiting competing alternatives in language but it remains unknown what allows predicting the linguistic hierarchy of inhibiting alternatives.

6. Conclusion

Our findings support the claim that the striatum holds a role in syntactic processing that is not restricted to its role in working memory. Although the nature of the syntactic impairment reported here should be further specified, this study shows that a syntactic impairment for selective conditions within syntactic processing occurs independently from working memory limitations. In particular, our results point to a deficit in the ability to apply infrequent rules in their appropriate context, after striatal lesions. Neuropsychological and functional imaging studies should further refine the biology of complex syntactic processing both in cortical and in sub-cortical structures.

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