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# The role of the striatum in phonological processing. Evidence from early stages of Huntington's disease

*Marc Teichmann*[a,b,c,*], *Isabelle Darcy*[d], *Anne-Catherine Bachoud-Lévi*[a,c] *and Emmanuel Dupoux*[b]

[a]*Neuropsychologie Interventionnelle, INSERM U955, IM3/Paris XII Créteil, France*
[b]*Laboratoire de Sciences Cognitives et Psycholinguistique, UMR8554, EHESS-ENS-CNRS, Departement d'Etudes Cognitives, Paris, France*
[c]*Department of Clinical Neurosciences, Henri Mondor Hospital, AP/HP, Créteil, France*
[d]*Department of Second Language Studies, Indiana University, Bloomington, USA*

## ARTICLE INFO

## ABSTRACT

The linguistic role of subcortical structures such as the striatum is still controversial. According to the claim that language processing is subdivided into a lexical memory store and a computational rule system (Pinker, 1999) several studies on word morphology (e.g., Ullman et al., 1997) and on syntax (e.g., Teichmann et al., 2005) have suggested that the striatum is specifically dedicated to the latter component. However, little is known about whether the striatum is involved in phonological operations and whether its role in linguistic rule application generalizes to phonological processing. We investigated this issue by assessing perceptual compensation for assimilation rules in a model of striatal disorders, namely in the early stages of Huntington's disease (HD).

In Experiment 1 we used a same–different task with isolated words to evaluate whether phoneme perception is intact in HD. In Experiment 2 a word detection task in phrasal contexts allowed for assessing both phoneme perception and perceptual compensation for the French regressive assimilation rule. Results showed that HD patients have normal performance with both phoneme perception in isolated words and regressive assimilation rules. However, in phrasal contexts they display reduced abilities of phoneme discrimination.

These findings challenge the striatum-rule claim and suggest a more fine-grained function of striatal structures in linguistic rule processing. Alternative explanatory frameworks of the striatum-language link are discussed.

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## 1. Introduction

There is compelling evidence that the role of the striatum extends beyond motor control to various cognitive domains involving executive functions (e.g., Brown et al., 1997) and language processing (e.g., Ullman, 2001). Such evidence also fits with structural findings showing that the striatum encompasses various neural circuits originating from higher

cognition cortices while presumably performing integrative computations on their respective functional input (Middleton and Strick, 2000; Lehéricy et al., 2004). Hence, with respect to language processing, the striatum has been claimed to be involved in rule-based computations which apply to lexical representations originating from temporal–cortical structures (Ullman, 2001). This proposal was also grounded on linguistic models which divide the human language faculty into two core components comprising a mental lexicon and a computational grammar. According to such models, the lexicon contains all linguistic idiosyncrasies such as phonemes, morphemes and words whereas the computational grammar holds the combinatorial rules which apply to the lexical input (Chomsky, 1965; Pinker, 1999). The claim about the role of the striatum in linguistic rule computation has been supported by various studies exploring both word morphology (Ullman et al., 1997; Ullman, 2001; Vannest et al., 2005; Teichmann et al., 2005, 2006) and syntax (Moro et al., 2001; Teichmann et al., 2005, 2008). However, it has not been verified in the domain of phonology and it remains controversial whether striatal structures genuinely hold a computational core function in language processing.

In word morphology, several studies have shown that patients with striatal damage (e.g., Huntington's disease, HD; Parkinson's disease, PD) are specifically impaired on the conjugation of regular verbs and/or non-verbs which depend on the application of rules (e.g., walk/walk-ed; splush/splush-ed). In contrast, lexical-based conjugation of irregular verbs (e.g., go/went) was shown to be near-normal in these patients (Ullman et al., 1997; Teichmann et al., 2005). Likewise, in syntax, several authors have reported that HD and PD patients are hampered on the comprehension of non-canonical sentences in which the usual word order is inverted as in passives or in object-relatives (Natsopoulos et al., 1993; McNamara et al., 1996; Kemmerer, 1999; Teichmann et al., 2005; Teichmann et al., 2008). Such types of sentences are claimed to depend on the application of syntactic movement rules (Chomsky, 1965, 1977, 1986) allowing for the mapping of their non-canonical surface structure (e.g., ''the boy$_{[3: \text{ theme}]}$ was kissed$_{[2: \text{ action}]}$ by the girl$_{[1: \text{ agent}]}$'') on the underlying canonical structure (''the girl$_{[1: \text{ agent}]}$ kissed$_{[2: \text{ action}]}$ the boy$_{[3: \text{ theme}]}$''). Impaired application of movement rules in patients sustaining striatal damage is thought to account for the incorrect assignment of thematic roles and thus to hamper access to the correct sentence meanings (''who [agent] does what [action] to whom [theme]''). Additional evidence for striatal involvement in linguistic rule application derives from functional imaging in both word morphology and syntax. Using fMRI with healthy adults, Vannest et al. (2005) have compared regular verbs and derived word forms (e.g., fit-ness, dream-less) with non-decomposable words showing that the processing of the former stimuli leads to increased activity in the striatum and in Broca's area. Likewise, in the domain of syntax, several authors have assessed healthy participants with sentences that did, or did not, contain phrase structure violations (e.g., ''the ice cream was in the *eaten''). They showed that covert reading of such ungrammatical sentences, followed by acceptability judgments, leads to the activation of striatal structures comprising the left caudate head (Moro et al., 2001) and of the left putamen (Friederici et al., 2003).

However, the view that the striatum specifically subserves linguistic rule application has been challenged by several authors suggesting that it impacts lexical processing. Using a conjugation task Longworth et al. (2005) have reported that patients sustaining striatal damage demonstrate lexical intrusions substituting semantically or phonological related verbs (e.g. bang-ed instead of slamm-ed). The same authors also used a priming paradigm with phonological related pairs (e.g., captive – captain) showing that, unlike controls, PD patients display significant priming effects. Thus, striatal damage may lead to difficulties in inhibiting inappropriate but phonologically related lexical items. In line with this lexical view, several studies reported that patients with striatal damage produce verbal paraphasias (Cambier et al., 1979; Damasio et al., 1982; Puel et al., 1984) and that they have poor performance in picture naming (e.g., Damasio et al., 1982; Cappa et al., 1983; Alexander et al., 1987; Wallesch, 1985; Démonet et al., 1991; Frank et al., 1996). Taken together, although various studies indicate that the striatum may play a role in language processing, its specific function within the lexicon/rule dichotomy remains a matter of debate. Extending the investigations beyond morpho-syntax to phonology by contrasting stored phoneme representations and phonological rule application may allow for clarifying this picture.

Unfortunately only few studies have explored whether the striatum impacts phonological processing. Several authors have investigated the production of speech sounds in patients with striatal damage such as HD, PD or stroke patients. They have reported that these patients have difficulties in speech articulation (Radanovic and Scaff, 2003), in prosody (Darkins et al., 1988) and in producing the correct timing for speech sounds (Ludlow et al., 1987) suggesting that the striatum impacts motor-related aspects of speech sound production. Interestingly, Speedie et al. (1990) showed that HD patients also have difficulties in perceiving speech sounds, namely in differentiating prosodic characteristics which distinguish statements from questions and commands. Yet, difficulties in the perception of prosody might not be tied to phonological disorders as such, but to more elementary difficulties in the perception of acoustic contours. Another way to approach phonological processes was adopted by Booth et al. (2007) who used fMRI to test healthy adults on a rhyming task. Participants were instructed to decide whether two written stimuli out of three rhymed or not. The analysis of the rhyming trials showed that these led to the activation of both cortical areas classically involved in phonological processing such as inferior frontal and superior temporal regions (see e.g., Poldrack et al., 1999; Indefrey and Levelt, 2004) as well as of the left putamen. However, as the authors acknowledged, rhyming judgments in the visual modality are a relatively complex task which involves decoding the orthographic stimuli, holding the phonological/articulatory information in working memory, and making an explicit determination about rhyming. Hence, such rhyming tasks make it difficult to determine whether the striatum subserves specific processes of phonology or whether it merely impacts on more general functions such as verbal working memory or explicit decision making. To our knowledge only two studies have specifically focused on the role of the striatum in phonological processing. Both assessed phonotactics, i.e., language-specific constraints that apply to

the sequential distribution of sounds in a given language. For example in English, the phoneme /d/ cannot precede /l/ at word onsets; hence, non-words with /dl/ onset clusters are phonotactically illegal. Tettamanti et al. (2005) tested healthy volunteers with phonotactically manipulated non-words comprising legal and illegal Italian phoneme strings. Participants made acceptability judgments while reading the non-words. Using a dopamine tracer and PET to measure striatal activity the authors showed that performance correlated with dopamine requirement in the left striatum. In particular, more accurate and faster phonological processing was associated with a reduced dopamine requirement in the left caudate head and the left putamen. Similarly, recording neural activity from depth electrodes in PD patients, Abdullaev and Melnichuk (1997) showed that the perception of phonotactically legal versus illegal non-words increased the firing rate of striatal cells. These two studies suggested that the striatum impacts the processing of phonological sequences which derive from statistical regularities of phoneme distribution. However, they did not provide direct evidence about the role of the striatum in applying phonological rules. Furthermore, both studies only manipulated written non-words and included few participants: seven healthy participants in the Tettamanti study and three PD patients in the Abdullaev study. Finally, the authors did not control whether phoneme representations as such were intact in their participants which makes drawing conclusions with respect to phonotactics difficult.

In the current study we assessed both the perception of phonemes and the application of phonological rules using auditorily presented stimuli with 15 HD patients at an early stage. HD is an inherited neurodegenerative disorder with primary neuronal dysfunction and death in the neostriatum (caudate and putamen) (Vonsattel et al., 1985; Peschanski et al., 1995). Hence, early stages of the disease can be considered as a reliable model of striatal dysfunction (see Kuhl et al., 1982; Mazziotta et al., 1987).

The perception of phonemes was assessed for two reasons. First, we wanted to ensure that the participants correctly perceive phonemic representations, which is indispensable for testing the application of phonological rules. Second, phoneme perception depends on the capacity to access stored phoneme categories and it may thus be considered as the equivalent of "lexical" processing. The application of phonological rules was tested through phoneme assimilation, which is a phonological process implying the propagation of phonetic features from one phoneme to the previous one, thereby triggering a partial or complete change in phonemic category. In English, there is a process of regressive place assimilation, which applies to dental stops and nasals, in the context of labial or velar obstruents. For instance, the final consonant of the word 'swee/t/' can change to /k/ or to /p/ according to its immediate right context: preceding a velar obstruent, /t/ changes to a velar /k/ (e.g., swee/k/ /g/irl); preceding a labial obstruent, it changes to a labial /p/ (e.g., 'swee/p/ /b/oy'). In French, place assimilation does not exist, but there is a comparable process of regressive voice assimilation which applies to obstruents when followed by voiced or unvoiced obstruents. For instance, the final consonant of the word "ro/b/" (dress) is devoiced to /p/ when followed by an unvoiced obstruent like in "ro/p/ /s/ale" (dirty dress).

Conversely, the final consonant of the word "ju/p/" (skirt) is voiced when followed by a voiced obstruent like in "ju/b/ /g/rise" (grey skirt). Such regressive assimilation seems to be obligatory at word boundaries (Féry, 2003; Snoeren and Segui, 2003; but see Dell, 1995 for word internal assimilation) and is difficult to inhibit in production unless a pause separates the two words. However, the application of phonological rules in word production is difficult to study in HD patients because of their articulation disorders. To avoid this problem we tested regressive assimilation in word perception given that healthy subjects compensate for assimilated forms by a process of 'inverse phonology'. Indeed, a context-sensitive process seems to undo the effect of phonological assimilation and thus, allows for the recovery of the underlying word forms via 'inverse rule application' (Gaskell and Marslen-Wilson, 1996, 1998; Gow, 2003; Darcy et al., in press). This process has been shown to be language-specific and applies to words as well as to non-words. In this paper, we used the word detection paradigm of Darcy et al. (in press), in which participants heard an auditorily presented stimulus [e.g., "robe" (dress)] which was followed by a sentence that contained the target stimulus and a context word [e.g., "robe... ceci est une robe sale (ro/b/ /s/al)"; dress...this is a dirty dress]. As a function of the context word, the target contained an assimilation change ("ro/p/ /s/ale"; dirty dress), an inappropriate voicing change, ("ro/p/ /n/oire"; black dress) or no change at all ("ro/b/ /r/ouge"; red dress). The assimilation was related to the voice feature or to the place feature and participants had to decide whether the target in the sentence was identical to the initial stimulus word. The authors showed that native French speakers apply language-specific assimilation rules in speech perception yielding 65% of "YES answers" for forms that were assimilated along the voicing contrast whereas word forms assimilated along the place contrast only yielded 18% of YES answers. Furthermore, low percentages of "YES answers" with inappropriate assimilated forms (7%) reflected normal capacities of phoneme perception.

In the present study we used a similar paradigm to assess phonological rule application and phoneme perception. We also tested phoneme perception in isolated words without phrasal contexts. HD patients were assessed with general parameters, including executive function scores as well as markers of disease progression comprising motor scores and overall functional capacities.

## 2. Method

### 2.1. Participants

Fifteen French speaking HD patients at stage I according to the "Total Functional Capacity Scale" (Shoulson, 1981), and 15 healthy volunteers participated in this study. HD patients were recruited in the out-clinic patients within the follow-up program of interventional therapy that was approved by the ethics committee of the Henri Mondor Hospital. HD patients had no previous neurological or psychiatric history other than HD. The HD diagnosis was genetically confirmed (Cytosine–Adenine–Guanine (CAG) repeats > 35). Healthy controls had no neurological or psychiatric disorders and were paired to

the HD patients according to their age and educational level (all Fs < 1). All participants gave informed consent. Demographic data are summarised in Table 1.

## 2.2. General assessment

All patients were evaluated using the UHDRS (Huntington Study Group, 1996) comprising Total Functional Capacity (TFC), motor scores, Literal Fluency, the Stroop test, and the Digit Symbol Code. Global intellectual capacities were tested using the Mattis Dementia Rating Scale (MDRS; Mattis, 1976). Functional data are summarised in Table 2.

## 2.3. Experimental tasks

Experiment 1 tested the perception of phonemes in isolated words. Participants made same–different judgments for auditorily presented words and non-words that either differed or not in one phoneme [e.g., mi/**m**/ – mi/**n**/ (*mime – mine*); lu/**b**/ – lu/**d**/ (non-word)].

Experiment 2 tested both the perception of phonemes and the application of assimilation rules in phrasal contexts. As in Darcy et al. (in press), participants made same–different judgments about auditorily presented stimulus-target pairs in which the target, surfacing in a sentence, was followed by a context word and did or did not contain a change of the last consonant. The changes were constructed by modifying the voice feature of the last consonant of the targets. Half of the changes represented regressive assimilations with respect to the initial consonant of the following context word (e.g., "robe… ceci est une ro/**p**/ /**s**/ale"; *dress…this is a dirty dress*) whereas the other half represented inappropriate changes (IC) corresponding to a simple phoneme change (e.g., "robe… ceci est une ro/**p**/ /**r**/ouge"; *dress…this is a red dress*). Because both conditions imply exactly the same feature changes they allowed for a direct comparison of two phonological capacities: "IC" assess phoneme perception via the ability to detect changes of the phoneme category whereas "assimilation changes (AC)" test the ability to inversely apply assimilation rules to phonemes that have changed their category in the context of regressive assimilation. Thus, in controls "IC" should yield "NO" answers whereas "AC" should yield "YES" answers.

Yet, both types of changes differ also at the level of phonetic contrasts. More particularly, in "AC" the two consonants never disagree in voicing whereas in "IC" half of

them do. In order to ensure that our task specifically probes for phonological rule processing, we included a second set of sentences using a non-native rule, namely assimilation of the place of articulation. According to the English place assimilation rule, and analogous to the voicing condition, the stimuli contained "AC" (e.g., "lune… ceci est une lu/**m**/ /**p**/âle"; *moon…this is a pale moon*), "IC" (e.g., "lune… ceci est une lu/**m**/ /**r**/ousse"; *moon…this is a red moon*) as well as unchanged targets (e.g., "lune… ceci est une lu/**n**/ /**j**/aune"; *moon…this is a yellow moon*). On the assumption that response differences between "IC" and "AC" follow from rule application, and not from phonetic factors, we expected such a difference only with voicing changes (native rule) but not with changes in the place of articulation (non-native rule).

Under the hypothesis that HD patients have rule disorders but intact access to stored phoneme representations, we predicted normal performance with phoneme perception in both isolated words (Experiment 1) and phrasal contexts (Experiment 2, "IC") but difficulties with the processing of phoneme assimilation (Experiment 2, "AC"). In particular, disorders with assimilation were expected to affect only the native rule, namely regressive voice assimilation, but not the phonologically irrelevant rule, namely regressive place assimilation.

## 2.4. Materials

Experiment 1 contained 20 stimuli comprising 10 French nouns [e.g., mime (mi/m/); *mime*] and 10 non-words (e.g., lu/b/). Non-words were constructed by changing one phoneme of an existing French noun [e.g. tube (*tube*) ⇒ **l**ube]. All stimuli were monosyllabic and the non-word stimuli were phonotactically legal. For 50% of the stimuli (5 nouns, 5 non-words), we constructed a target stimulus by modifying the last consonant along the voicing dimension (e.g., lu/**b**/ – lu/**p**/) (3 nouns, 2 non-words) or along the place of articulation dimension (e.g., rou/**p**/ – rou/**k**/) (2 nouns, 3 non-words). For the remaining 50%, the stimulus and the target stimulus were identical.

Experiment 2 contained 32 French monosyllabic nouns ending in an obstruent consonant. For each of these, we constructed three sentences that contained either the unchanged form of the noun or a form featuring a change in the last consonant. We will refer to these forms as the target stimuli. In all sentences the target stimulus was followed by a context word (i.e., an adjective). The initial consonant of the

### Table 2 – Clinical performance in HD patients

| | HD | Normal |
|---|---|---|
| Total Functional Capacity (TFC) | 11.9 ± .9 | 13 |
| UHDRS motor score | 27.1 ± 15.8 | 0 |
| Stroop colour/words | 27.7 ± 9.9 | >35[α] |
| Fluency "P", "R", "V" (in 2 min)[a] | 46.0 ± 22.7 | >56[β] |
| Symbol Digit Code | 30.1 ± 10.8 | 37[δ] |
| MDRS | 130.6 ± 9.9 | >136[λ] |

UHDRS = United Huntington Disease Rating Scale.
Normal values are issued from: [α]Mattis, 1976; [β]Golden, 1978; [δ]Cardebat et al., 1990; [λ]Wechsler, 1981.
a Literal fluency with the three letters "P", "R" and "V" measured during 2 min.

### Table 1 – Demographic data of HD patients and controls

| | HD | Controls |
|---|---|---|
| N | 15 | 15 |
| Sex | 10M/5F | 10M/5F |
| Age (years) | 48±7.8 | 48.5±8.4 |
| Years of education | 13.6±3.5 | 13.8±2.8 |
| Handedness | 13R/2L | 13R/2L |
| Evolution duration (years) | 4.7±2.9 | ////////// |
| CAG repeats | 43.6±2.8 | ////////// |

CAG repeats = repetition of the nucleotide triplet Cytosine–Adenine–Guanine. HD patients have more than 35 repetitions of this triplet within the Huntingtine gene of chromosome 4.

context word either elicited or did not elicit assimilation of the target. This yielded three types of target stimuli: "AC", "IC" and non changed forms (NC). Two conditions, namely voicing changes and changes in place of articulation were used, each containing the same number of AC ($N = 16$), IC ($N = 16$) and NC ($N = 16$). In the voicing condition, the AC and the IC corresponded to a voicing change of the last consonant whereas in the place condition, the consonantal change concerned the place of articulation. Altogether, we used 96 test sentences, 48 in the place condition and 48 in the voicing condition with three target types in each of the conditions. The materials are summarised in Table 3.

In addition, we selected 12 filler nouns, for which we constructed 12 filler sentences containing 12 filler targets. The filler targets were constructed by changing the last consonant of the filler noun (no AC) or by replacing the filler noun with another word.

Finally, we constructed the stimuli for two training sets. The first training set comprised 10 nouns and 10 non-words. We used 20 sentences containing the target stimuli in the sentence-final position (no context word). The target stimuli contained a change (or not) in the last consonant of the noun/ non-words. The second training set comprised 18 stimuli that were constructed like the filler stimuli.

The nouns of the voicing and the place condition were matched for their token frequency according to the Brulex database [Content et al., 1990; place condition: 42.38 per million, voicing condition: 48.37 per million; $t(15) = .4$, $p > .1$]. Furthermore, the different sentences were matched for their number of words [place condition: $N = 8,7$; voicing condition: $N = 7,5$; $t(47) = 1.6$, $p > .1$] as well as for the phrasal position of the target [$t(47) = -1.23$, $p > .1$].

All stimuli were recorded by native French speakers. In Experiment 1 the nouns/non-words were recorded by a male speaker and the target stimuli were recorded by a female speaker. In Experiment 2 the nouns were recorded by a male speaker and the sentences were recorded by a female speaker. All stimuli were digitized at a 16,000 Hz sampling rate for binaural presentation over headphones.

### 2.5. Procedure

In Experiment 1 each noun/non-word was displayed three times followed by the target stimulus. Participants were

**Table 3 – Target stimuli and context words comprising 3 target types (AC, IC, NC) and two articulation contrasts (voicing, place)**

| Target type | Target "robe" /rob/ (*dress*) | Target "lune" /lyn/ (*moon*) |
|---|---|---|
| | Native (voicing condition) | Non-native (place condition) |
| AC | ro/**p**/ /s/ale (*dirty dress*) | lu/**m**/ /**p**/ale (*pale moon*) |
| IC | ro/**p**/ /**n**/oire (*black dress*) | lu/**m**/ /**r**/ousse (*red moon*) |
| NC | ro/**b**/ /**r**/ouge (*red dress*) | lu/**n**/ /**j**/aune (*yellow moon*) |

instructed to decide whether the noun/non-word and the target stimulus were the same and to indicate their decision by selecting a YES/NO answer. Feedback was provided 3000 msec after the target stimulus onset. The presentation order was the same for each participant.

Experiment 2 was run after Experiment 1. It was composed of two training sets and the test set. Feedback was given only for the training sets. The procedure was the same for the training sets and for the test set: the noun stimulus was followed by the sentence after a 500 msec interval. Participants were instructed to decide whether the noun stimulus and the target stimulus of the sentence were the same and to indicate their decision by selecting a YES/NO answer. In order to allow for several pauses, the test set was subdivided into three stimuli lists each containing 36 trials. Each training set and the three stimuli lists of the test set were followed by a short pause, and the experiment was continued when the participant felt ready. The presentation order of the three stimuli lists of the test set was the same for each participant.

## 3. Results

Experiment 1: Performance was similar in controls (97% ± .1 correct) and HD patients (94% ± .3 correct) [$t(28) = 1.47$, $p > .1$].

Experiment 2: Analyses of variance (ANOVAs) were conducted by participants (F1) and by items (F2) with "detection rate" (% of "YES answers") as the dependent variable. The independent variables were "group" (HD, controls), condition (voicing, place) and target type (AC, IC, NC). To detect deviating stimuli, we calculated in controls for each stimulus the mean values of detection rates with NC and with IC. This led to the exclusion of one stimulus which deviated by more than 2 standard deviations from the mean value of IC.

Overall detection rates were higher in HD (67% ± 27.3) than in controls [48% ± 39.1; $F1(1,28) = 63.4$, $p < .0001$; $F2(1,29) = 78.1$, $p < .0001$]. There was a condition effect [$F1(1,28) = 47.9$, $p < .0001$; $F2(1,29) = 60.3$, $p < .0001$], a target type effect [$F1(2,56) = 307.5$, $p < .0001$; $F2(2,58) = 328.0$, $p < .0001$] and a target type × condition interaction [$F1(2,56) = 52.5$, $p < .0001$; $F2(2,58) = 31.3$, $p < .0001$]. There was also a group × target type interaction [$F1(2,56) = 35.0$, $p < .0001$; $F2(2,58) = 39.5$, $p < .0001$] but no group × condition interaction (both $F < 1$) and no triple group × condition × target type interaction [$F1(2,56) = 3.0$, $p = .06$; $F2(2,58) = 1.9$, $p > .1$]. The results are summarised in Fig. 1.

Post hoc analyses were used to assess two contrasts. First, we compared detection rates with AC, IC and NC in the voicing and the place condition. For AC, controls and HD patients yielded more "YES answers" in the former than in the latter condition [controls: $F1(1,14) = 92.7$, $p < .0001$; $F2(1,29) = 49.7$, $p < .0001$; HD: $F1(1,14) = 23.1$, $p < .0001$; $F2(1,29) = 26.7$, $p < .0001$; group × condition interaction: $F1(1,28) = 3.0$, $p > .1$; $F2(1,29) = 2.7$, $p > .1$] suggesting that all participants applied the native voicing rule but hardly the non-native place rule. For IC, controls yielded more "YES answers" in the voicing condition than in the place condition only in the analysis by items [$F1(1,14) = 9.1$, $p = .009$] but not in the analysis by participants [$F2(1,29) = 3.3$, $p = .076$]. In HD patients there was no difference between the voicing and the place condition [$F1(1,14) = 1.4$, $p > .1$; $F2(1,29) = 1.3$, $p > .1$]. There was no
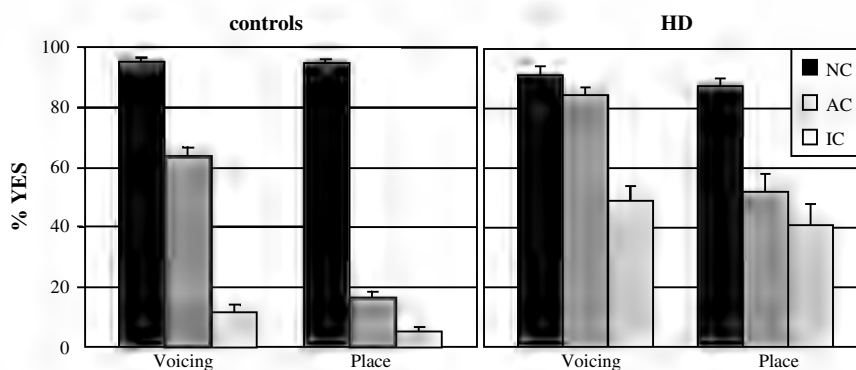
**Fig. 1 – YES answers in controls and HD for the 3 target types in the voicing condition and in the place condition.**

group × condition interaction (both F's < 1). For NC, controls and HD patients yielded similarly high rates of "YES answers" in the voicing and in the place condition [controls: both F's < 1; HD: $F_{1(1,14)} = 1.3$, $p > .1$; $F_{2(1,29)} = 1.5$, $p > .1$; group × condition interaction (both F's < 1)]. Second, we compared detection rates of AC and IC in both the voicing and the place condition. In the voicing condition, AC yielded more "YES answers" than IC in both controls [AC 64% ± 11.8, IC 12% ± 8.8; $F_{1(1,14)} = 138.1$, $p < .001$; $F_{2(1,28)} = 52.3$, $p < .001$] and HD patients [AC 84% ± 10.6, IC 49% ± 19.3; $F_{1(1,14)} = 33.3$, $p < .001$; $F_{2(1,28)} = 33.4$, $p < .001$]. There was a group × target type interaction only in the analysis by participants [$F_{1(1,28)} = 4.5$, $p = .04$] but not in the analysis by items [$F_{2(1,28)} = 2.8$, $p > .1$]. In the place condition, AC yielded more "YES answers" than IC in controls [AC 17% ± 7.3, IC 5% ± 5.2; $F_{1(1,14)} = 81.0$, $p < .001$; $F_{2(1,30)} = 13.6$, $p = .001$]. HD patients displayed more "YES answers" for AC only in the analysis by participants [AC 52% ± 22.7, IC 41% ± 27.6; $F_{1(1,14)} = 8.3$, $p = .01$] but not in the analysis by items [$F_{2(1,30)} = 2.5$, $p > .1$]. There was no group × target type interaction (both F's < 1). Finally, we calculated

by participants the magnitude of the difference between detection rates of AC and IC in both the voicing and the place condition. In both controls and HD patients, this difference was larger in the voicing than in the place condition [controls: voicing 51% ± 17.0, place 11% ± 4.8, $F_{(1,14)} = 63.7$, $p < .001$; HD: voicing 36% ± 23.9, place 11% ± 15.2, $F_{(1,14)} = 11.0$, $p = .005$]. There was no group × condition interaction [$F_{(1,28)} = 3.2$, $p = .08$].

In the aim to provide a marker for the ability of both phoneme discrimination and phoneme assimilation we determined for each participant a "discrimination index" and an "assimilation index". The discrimination index was calculated using the mean rate of correct answers in both Experiment 1 and Experiment 2 (NC and IC). The assimilation index was calculated using "YES answers" with NC and IC as the base line which was compared with AC ([AC − IC/NC − IC] × 100). This ratio would be 100% if assimilation is applied for all AC whereas it would be at "zero" if there is no assimilation at all.

ANOVA's with the dependent variable "discrimination index" used "group" (controls, HD) as the independent variable. In Experiment 1, the discrimination index was similar in HD patients and controls (F < 1). In Experiment 2, the discrimination index was lower in HD (72%) than in controls [93%, $F_{1(1,28)} = 36.9$, $p < .001$] suggesting that HD patients have difficulties with phoneme perception in phrasal contexts. ANOVA's with the dependent variable "assimilation index" used "group" (controls, HD) and "condition" (voicing, place) as independent variables. HD patients had an overall higher assimilation index (50%) than controls [37%, $F_{1(1,28)} = 12.1$, $p = .002$]. The index was higher for the voicing condition (68%) than for the place condition [18%, $F_{1(1,28)} = 64.2$, $p < .001$]. There was no group × condition interaction (F1 < 1). Post hoc analyses for the voicing and the place condition revealed that the assimilation index was similar in HD patients and controls for both conditions [voicing: HD 76%, controls 61%, $F_{(1,28)} = 3.8$, $p = .06$; place: HD 23%, controls 13%, $F_{(1,28)} = 2.3$, $p = .13$] suggesting normal assimilation rule application in HD. The results are summarised in Fig. 2.

## 4. Discussion

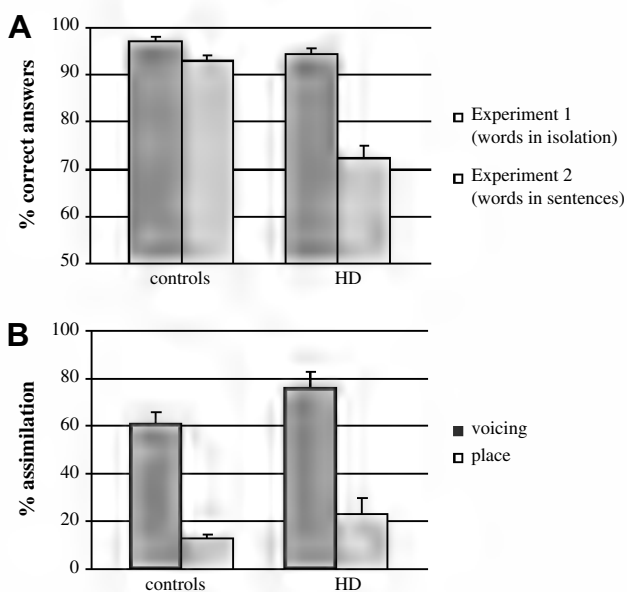We investigated the role of the striatum in phonological processing by assessing assimilation rule application and phoneme perception in early stages of HD. Experiment 1



**Fig. 2 – Discrimination index (A) and compensation index (B) in HD and controls.**

showed that HD patients are unimpaired in the perception of phonemes during the processing of isolated words and non-words. Experiment 2 assessed phoneme perception and rule application in phrasal contexts. Performance patterns were similar in controls and HD patients. In particular, both accepted AC that refer to consonant voicing more often than AC that refer to the place of articulation. Furthermore, the magnitude of the difference between AC and IC was more important in the voicing condition than in the place condition, suggesting that controls as well as HD patients apply the native voicing rule but hardly the non-native place rule. Consistently, assimilation indexes were higher in the voicing than in the place condition in both controls and HD patients. Our interpretation, according to which these findings genuinely reflect language-dependent rule application, and not language-universal phonetic differences between voicing and place contrasts, is reinforced by a recent study of Darcy et al. (in press). Using exactly the same stimuli and procedure the authors found that late English learners of French display the inverse performance pattern, compensating more for place than for voicing contrasts, which corresponds to the behaviour of English monolinguals listening to English sentences. Furthermore, more advanced learners reverse this effect and display the French pattern like our controls and HD patients. However, the behaviour of HD differed from controls in that they perceive changed targets more often as being identical to the initial noun stimulus suggesting difficulties in perceiving phoneme changes in phrasal contexts. This is also reflected by the mean values of discrimination indexes which are lower in HD patients than in controls for Experiment 2 (phrasal context) but similar for Experiment 1 (words in isolation). Taken together, our results suggest that the application of phonological assimilation rules is intact in HD. Likewise, phoneme perception is normal with isolated words but seems to be hampered in phrasal contexts.

These findings appear to be at odds with previous claims about the involvement of the striatum in language processing. They show that patients with striatal damage are not impaired in linguistic rule application, at least with respect to assimilation rules, nor in accessing stored language representations, namely phoneme categories. In contrast, the striatum seems to be involved in perceiving phonemes in phrasal contexts, suggesting damage of short-term memory capacities which are engaged when listening to sequences of words. This latter finding fits with a recent study of Jacquemot et al. (2006) which reported that two patients with extensive left hemisphere damage were impaired when they had to detect phoneme changes in the context of sentences but not during the perception of isolated words. The authors have shown that this deficit was neither due to the increased speaking rate of words in sentences, nor to the forward or backward masking effect of the sentences' surrounding words but to the increased load on phonological short-term memory. Hence, one possibility is that the striatum subserves short-term memory processes that are used in online phonological operations. This interpretation would be consistent with previous claims stating that the role of the striatum in language processing is directly tied to its involvement in verbal working memory capacities (Lieberman et al., 1992;

Gabrieli, 1995; Hochstadt et al., 2006). However, striatal damage might neither be related to impaired access to phonemes in phrasal contexts, nor to disorders of the phonological short-term memory, but to a reduction of general resources such as attention. Indeed, the pattern of results in HD can be characterized as a response bias in favour of real words: they had no difficulties accepting unchanged word forms but failed to reject changed forms that phonetically corresponded to non-words. This may indicate that HD patients do not engage in a post-access checking mechanism and only use the best fitting real word (from a phonetic or semantic point of view), especially when their attention is engaged in online comprehension. We should note that the detection task in phrasal contexts is intrinsically more difficult even for controls, as they made twice as many errors in sentences as compared to words in isolation (3% in isolation *vs* 7.5% in sentences). It is then possible that an attentional deficit in HD patients has a multiplicative effect on task difficulty.

In each case, our findings contrast sharply with previous studies showing that HD patients are specifically impaired on rule application in both the domain of morphology and of syntax (Ullman et al., 1997; Teichmann et al., 2005, 2006, 2008). Likewise, our results reflecting normal access to stored phoneme representations in isolated words do not fit with claims stating that the striatum subserves linguistic/lexical memory processes (e.g., Damasio et al., 1982; Butters et al., 1986; Wallesch and Papagno, 1988; Frank et al., 1996; Longworth et al., 2005). In order to verify the previous findings in the domain of morphology and syntax, we assessed lexical and rule capacities in our HD population confirming that morphological and syntactic rule application, but not lexical access, is impaired.[1] An explanation for this dissociated picture could be that the striatum is not uniformly involved in linguistic rules but that it specifically taps certain kinds of rule computations. Indeed, phonological assimilation rules differ from morphological and syntactic movement rules because they do not apply recursively but locally and thus independently from memory buffers that hold intermediate computations. Accordingly, it has been shown that phonological rules can be applied in a parallel fashion to a string of phonemes using a simple finite-state transducer (Johnson, 1972). Morphological and syntactic rules, in contrast, require a more complex processing architecture. This is clearly visible in the case of syntax, which cannot be processed by a finite-state architecture but requires memory buffers to enable recursive processing and manipulation of long-distance dependencies. Likewise, in morphology, HD

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[1] We tested 7 out of the 15 HD patients using lexicon/rule tasks from a previous study of ours (see Teichmann et al., 2005). All seven patients were impaired on rule application in both morphology and in syntax, as reflected by poor performance with the conjugation of non-verbs (52% errors on subregular non-verbs) and the comprehension of sentences containing syntactic movement (20% errors on passives and object-relatives). In contrast they were unimpaired on lexical processes as reflected by normal performance with the conjugation of irregular verbs (5% errors) and the comprehension of canonical sentences (2% errors on actives and subject-relatives).

patients are impaired with non-verbs, which require a two-step computation: extraction of the root and application of the rule. Thus, one plausible hypothesis may be that the striatum is specifically involved in rules requiring memory buffers by maintaining linguistic information in a language-related short-term memory. Yet, it should be noted that previous findings have shown that not all morphological and syntactic rules are affected to the same degree. Indeed, HD patients are especially impaired with non-verbs responding to sub-regularities which depend on the application of relatively infrequent and thus poorly automatized rules (e.g., Teichmann et al., 2005, 2006). Likewise, in syntax only infrequent movement rules, which are required for passives and object-relatives are impaired whereas the processing of actives and subject-relatives is relatively preserved (e.g., Natsopoulos et al., 1993; McNamara et al., 1996; Kemmerer, 1999; Teichmann et al., 2005, 2008). Thus, an alternative hypothesis may be that infrequent and poorly automatized rule operations are highly sensitive to striatal damage. In this vein, the striatum may genuinely hold rule devices which break down when neural damage extensively hampers the linguistic functioning of the striatum. Studying phonological capacities in HD at more advanced stages or in stroke patients with extensive striatal damage should allow clarifying this picture. Note that this latter hypothesis has already received some support from previous findings, suggesting that the striatum is involved in the processing of phonotactic constraints (Tettamanti et al., 2005; Abdullaev and Melnichuk, 1997). Given that phonotactic constraints apply locally without memory constraints and given that they are the results of both statistical regularities in the phonological lexicon and the application of phonological rules, the striatum may genuinely impact phonological rule application.

In conclusion, our findings suggest that the striatum impacts language processing in several ways. First, its implication in non-language-specific functions such as attentional resources may have a general impact on language performances. Second, the striatum presumably subserves phonological short time memory capacities which underpin accurate word perception in phrasal contexts. This latter role may also be involved in morphological and syntactic rule application which depends on the maintaining of intermediate language chunks such as morphemes and grammatical groups. Yet, we suggest that the striatum may also hold a genuine role in linguistic rule computation applying to particular kinds of morpho-syntactic and eventually phonotactic rules. Further studies should help to precise the phonological function(s) of the striatum and to characterise the specific type of rules it subserves.

## Acknowledgments

## Appendix

| Experiment 1 | | |
| --- | --- | --- |
| Stimulus | Target | Phoneme change |
| bague | bac | + |
| seize | seize | − |
| bec | bete | + |
| pique | pique | − |
| mime | mine | + |
| roupe | rouque | + |
| cage | cage | − |
| sigue | sique | + |
| tente | tente | − |
| brite | brite | − |
| pouche | pouje | + |
| paze | paze | − |
| nappe | natte | + |
| mousse | mousse | − |
| bronne | brome | + |
| noque | noque | − |
| lube | lude | + |
| beche | beige | + |
| chame | chame | − |
| gleche | gleche | − |

| Experiment 2 | | |
| --- | --- | --- |
| Stimulus | Sentence containing the target | Target type |
| *Voicing condition* | | |
| **Robe** | La petite fille jette sa **rope** sale. | AC |
| | Elle n'aime pas sa **rope** noire. | IC |
| | Elle préfère la **robe** rouge. | NC |
| **Coude** | Il a eu le **coute** tordu pendant quinze jours. | AC |
| | Il avait un **coute** raidi depuis son accident. | IC |
| | Il a eu le **coude** meurtri lors de la chute. | NC |
| **Globe** | Au plaond on voit tourner un **glope** pailleté. | AC |
| | Il a un **glope** lumineux dans sa chambre. | IC |
| | La guirlande entoure un **globe** miroitant. | NC |
| **Neige** | J'ai horreur de la **neiche** poudreuse. | AC |
| | Les rues sont pleines de **neiche** marron. | IC |
| | Il tombe de la **neige** mouillée. | NC |

## Experiment 2 (continued)

| Stimulus | Sentence containing the target | Target type |
|---|---|---|
| Lave | Des tonnes de **lafe** pâteuse descendent de la montagne. | AC |
| | Une couche de **lafe** rugueuse recouvre tout. | IC |
| | Lentement, la **lave** mouvante se dirige vers la mer. | NC |
| Nuage | Le ciel se couvre de **nuaches** chargés. | AC |
| | On voit quelques **nuaches** nacrés qui se forment. | IC |
| | Ces **nuages** rosés donnent une lumière très spéciale | NC |
| Cuve | Le liquide se trouve dans une **cufe** fendue. | AC |
| | L'apprenti a renversé la **cufe** remplie. | IC |
| | Ils emmènent cette **cuve** mobile avec eux. | NC |
| Badge | On leur a donné un **badche** parfumé. | AC |
| | Les employés portent un **badche** ravissant. | IC |
| | Cette société produit des **badges** métalliques. | NC |
| Nappe | Elle est belle, cette **nabbe** brodée. | AC |
| | J'ai mis la **nabbe** rustique sur la table. | IC |
| | Elle s'est offert une belle **nappe** rayée. | NC |
| Faute | Personne n'a remarqué cette **faude** discrète. | AC |
| | Il commet une **faude** légère en début de jeu. | IC |
| | Il y a eu une **faute** majeure mais sans conséquences. | NC |
| Route | La voiture roule sur une **roude** dangereuse. | AC |
| | Tous les matins, il prend une **roude** nationale. | IC |
| | C'est une **route** magnifique. | NC |
| Chèque | le **chègue** volé n'a pas été encaissé. | AC |
| | Le **chègue** reçu n'est pas couvert. | IC |
| | le **chègue** mensuel a été débité. | NC |
| Plaque | Il a posé une petite **plague** brillante à sa porte. | AC |
| | Une épaisse **plague** rouillée sert de porte. | IC |
| | Une petite **plague** noircie indique son nom. | NC |
| Couche | Il faut enlever la **couje** jaunie avant de continuer. | AC |
| | On voit partout une **couje** marron. | IC |
| | Tout disparaît sous cette **couche** neigeuse. | NC |
| Cape | Les sorcières portent une **cabe** grise pour aller au bal. | AC |
| | Il a mis sa **cabe** neuve sur le dossier de la chaise. | IC |
| | Une **cape** longue protège mieux du froid. | NC |

## Experiment 2 (continued)

| Stimulus | Sentence containing the target | Target type |
|---|---|---|
| Lac | Les **lags** gelés sont plus dangereux qu'on ne croit. | AC |
| | Les **lags** nordiques sont souvent magnifiques. | IC |
| | Un **lac** limpide embellit la propriété. | NC |

*Place condition*

| Stimulus | Sentence containing the target | Target type |
|---|---|---|
| Bête | Il y a une **bêpe** poilue dans la cave. | AC |
| | Il a vu une **bêpe** féroce qui lui a fait peur. | IC |
| | Il a découvert une **bête** nuisible dans ses rosiers. | NC |
| Bottes | Il pleuvait très fort et il a mis ses **bopes** pointues. | AC |
| | Il n'y a que ces **bopes** rayées pour aller avec ton pantalon. | IC |
| | Elle a mis ses **bottes** montantes pour sortir. | NC |
| Boîte | Elle garde son argent dans une **boike** carrée. | AC |
| | Il y a une **boike** fermée sur la table. | IC |
| | Le cadeau était dans une **boite** marron. | NC |
| Chouette | Il a recueilli et apprivoisé une **choueke** craintive. | AC |
| | J'ai vu une **choueke** sauvage traverser le jardin. | IC |
| | Hier, il a porté sa **chouette** malade au zoo. | NC |
| Guide | Ce **guibe** bourru critique tout ce qu'il voit. | AC |
| | L'agence a renvoyé le **guibe** vulgaire ce matin. | IC |
| | Le **guide** raciste ne veut pas prendre le groupe d'étrangers. | NC |
| Stade | la ville veut remplacer le **stabe** bétonné par un ensemble neuf. | AC |
| | Le **stabe** démodé doit bientôt disparaître. | IC |
| | Il préfère aller s'entraîner dans ce **stade** rénové. | NC |
| Mode | Cette année, la **mogue** guerrière fait fureur. | AC |
| | On ne parle que de **mogue** zoulou. | IC |
| | Les émissions sur la **mode** locale m'énervent. | NC |
| Ride | Une **rigue** gracieuse rendait son visage mémorable. | AC |
| | Il a une **rigue** discrète au menton depuis toujours. | IC |
| | A force de rire, il a des **rides** légères au coin des yeux. | NC |
| Moine | Frère Jean est vraiment un **moime** bavard. | AC |
| | C'est un **moime** serviable qui nous a fait la visite. | IC |
| | Ce monastère est dirigé par un **moine** rusé. | NC |

| Experiment 2 (continued) | | |
| --- | --- | --- |
| Stimulus | Sentence containing the target | Target type |
| Lune | On ne voit rien, la **lume** pâle est cachée par les nuages. | AC |
| | Cette nuit, la **lume** rousse est étonnante. | IC |
| | la **lune** jaune éclaire parfois plus que d'habitude. | NC |
| Prunes | Il a ramassé des **prumes** pourries tombées de l'arbre. | AC |
| | Sa maman lui interdit de manger des **prumes** sucrées. | IC |
| | On ne trouve pas de **prunes** juteuses sur le marché. | NC |
| Reine | En général, les **reimes** paresseuses sont rares. | AC |
| | Jeanne était une **reime** respectée qui a vécu longtemps. | IC |
| | Ils ont élu une **reine** généreuse à la tête du pays. | NC |
| Dune | Il admirait cette longue **dume** brumeuse. | AC |
| | Il faut grimper sur cette **dume** sauvage. | IC |
| | L'oasis se trouve derrière cette **dune** lointaine. | NC |
| Ruine | Cette **ruime** baroque est de toute beauté. | AC |
| | Nous avons visité une **ruime** celebre. | IC |
| | Il y a relativement peu de **ruines** romaines. | NC |
| Trône | C'est cet artisan qui a sculpté le **trôme** princier. | AC |
| | Le **trôme** royal est situé au centre de la pièce. | IC |
| | De ce peuple, il ne reste que ce **trône** rocheux. | NC |
| Zone | Il habite dans une **zome** portuaire. | AC |
| | Une **zome** fluviale est toujours dangereuse. | IC |
| | Cette **zone** rurale est plus calme que les autres. | NC |

NC = non changed forms.
Deviating and excluded stimulus: "faute".

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