Word processing in Parkinson's disease is impaired for action verbs but not for concrete nouns

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Abstract

Recent studies have demonstrated that processing of action words recruits cortical motor regions that are also involved in the planning and execution of the actions words refer to. The functional role of these regions in word understanding remains, however, to be clarified. The present study investigates this issue by examining the impact of Parkinson's disease (PD) on lexical decision performance for action words, relative to concrete nouns, in a masked priming paradigm. Priming effects for the two word categories were measured in non-demented PD patients off and on dopaminergic treatment, and in healthy participants. Our results revealed that although overall performances did not differ between verbs and nouns, priming effects showed a clear dissociation between word categories. While priming for concrete nouns was not affected by Levodopa intake, it dissociated as a function of treatment for action verbs. No priming was actually obtained for action verbs in PD patients off dopaminergic treatment. Following Levodopa intake, this deficit recovered, however, because priming effects for verbs became comparable to those for concrete nouns and similar to performance of healthy participants. Overall, this study thus brings compelling evidence that processing lexico-semantic information about action words depends on the integrity of the motor system.
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1. Introduction

Recent investigations of the cortical network that underlies language abilities have revealed that the same brain areas that are involved in the planning and execution of body movements are also partly recruited when words describing these movements are perceived (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Boulenger et al., 2006; Buccino et al., 2005; Hauk, Johnsrude, & Pulvermüller, 2004; Oliveri et al., 2004; Nazir et al., 2008; Pulvermüller, Shtyrov, & Ilmoniemi, 2005; Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005; Tettamanti et al., 2005). Using fMRI, Hauk et al. (2004), for instance, have shown that premotor and motor cortex are active during passive reading of words that refer to actions performed

with different body parts. More intriguingly, this language-related cortical activity followed the somatotopy of cortical motor regions and thus varied spatially depending on whether the words denoted actions performed with the face, arms, or legs (see also Tettamanti et al., 2005 for related findings using sentences). A similar pattern of results was also reported by Aziz-Zadeh et al. (2006), who showed overlapping motor activation between passive reading of action-related sentences and action observation. Using TMS, Buccino et al. (2005) further substantiated these findings by revealing modulations of left motor cortex excitability (i.e. reduced amplitude of motor-evoked potentials) during listening to hand- and leg-action-related sentences when TMS was concurrently applied to the corresponding motor areas.

However, while the results of these studies clearly demonstrate that motor regions are recruited during processing of action-related language, they do not allow clarifying the crucial question about the functional role of these areas in language: are cortical motor regions critical to word understanding? Part of this shortcoming comes from the fact that most previous

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studies cannot clearly determine when, subsequent to word onset, language-related motor activity actually emerges. As a matter of fact, activity in motor regions could simply arise *consecutively* to word identification, and once the word is understood, it could trigger motor imagery of the action it describes. Mental motor imagery is indeed known to involve motor areas (Jeannerod, 1994; Jeannerod & Frak, 1999).

Two recent studies (Boulenger et al., 2006; Pulvermüller, Shtyrov et al., 2005) nevertheless provided robust evidence that language-related motor activity occurs early following word onset. Using MEG, Pulvermüller, Shtyrov et al. (2005) could show that, at 130–150 ms after stimulus onset, spoken face- and leg-related action words elicited activity in peri-sylvian language areas. This activity was almost immediately followed by a short-lived somatotopic activity along the motor strip (170–200 ms post-stimulus). Given that lexico-semantic effects generally occur within 200 ms following word presentation (Hauk et al., 2006; Preissl, Pulvermüller, Lutzenberger, & Birbaumer, 1995; Pulvermüller, Lutzenberger, & Preissl, 1999; Sauseng, Bergmann, & Wimmer, 2004; Sereno & Rayner, 2003), the authors suggested that motor regions may play an active role in action word comprehension. In a similar vein, Boulenger et al. (2006), who performed continuous and online analyses of fine-grained movement kinematics while participants were engaged in a lexical decision task, demonstrated that within the same early time window after word onset (<200 ms), processing of action verbs interfered with the concurrent execution of a reaching movement (i.e. reduced amplitude and longer latency of the wrist acceleration peak for verb- relative to noun-stimuli). These interference effects were interpreted as reflecting competition for common resources between processes involved in movement execution and processes involved in action word encoding.

A more definitive test of the role of motor regions in language comprehension, however, would come from neuropsychological studies that show selective deficits in action word processing following lesions in motor regions of the brain—or in relation to movement disorders in general (see Mahon & Caramazza, 2005). Selective deficits for verbs have indeed been described in patients with progressive supranuclear palsy (Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994) or with motor neuron disease (Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001; Bak & Hodges, 2004). In addition, Bak et al. (2006) recently reported the case of a familial occurrence of selective deficit of verb processing in association with movement disorder. The present study aimed at corroborating these findings by assessing the impact of Parkinson's disease (PD) on action word processing.

PD is a neurodegenerative disease caused by a dopaminergic deficiency of the nigrostriatal pathway, primarily characterized by motor disorders (i.e. akinesia/bradykinesia, rigidity and tremor), although deficits in cognitive functions and subtle semantic language deficits have also been reported (for a review, see Pillon, Boller, Levy, & Dubois, 2001). Neuroimaging studies have revealed that during movement execution, regions involved in motor preparation, which receive strong projection from the striato-frontal loop (Alexander, DeLong, & Strick, 1986; DeLong, 1990), are under-activated in PD patients (Jahanshahi

et al., 1995; Jenkins et al., 1992; Playford et al., 1992; Rascol et al., 1992, 1994). This impairment improves, however, following dopaminergic treatment (Haslinger et al., 2001), which increases dopamine levels in the striatum and restores the function of the basal ganglia. Electrophysiological studies have also shown that the amplitude of pre-movement activity is reduced in PD patients (Dick et al., 1987; Jahanshahi et al., 1995; Oishi, Mochizuki, Du, & Takasu, 1995; Shibasaki, Shima, & Kuroiwa, 1978). Here again, the deficit recovers after Levodopa ingestion (Dick et al., 1987). If premotor and motor regions that are involved in movement preparation and execution play also a role in action word understanding, PD patients deprived of dopaminergic treatment should show selective deficits in processing these words but not in processing other classes of words, such as concrete nouns. Furthermore, Levodopa intake, which re-establishes normal activation level in premotor and motor areas via the striato-frontal loop, should not only restore motor deficits but also the selective deficit for action verbs.

To test this, the present study compares lexical decision latencies (i.e. the time it takes to decide whether a letter string is a word or not) for action verbs and concrete nouns of non-demented PD patients (off and on dopaminergic treatment) using a masked priming paradigm. In such a paradigm, a prime-word is presented in close spatial and temporal proximity with other visual stimuli, so that it is not consciously perceived (i.e. it is masked). A target-word, which is identical to the prime but written in different case (TABLE–table), is subsequently displayed and participants have to indicate as quickly as possible whether the target is a word. Masked prime-words, though not consciously perceived, pre-activate essential parts of the cerebral networks for word processing (Dehaene et al., 2001) and thereby lead to considerable reduction in response times to immediately following target words (Ferrand, Grainger, & Segui, 1994; Forster & Davis, 1984). Given that visual features of prime and target differ, cross-case priming effects are based on activation of lexical-semantic representation of words. Moreover, in as much as masked primes are not consciously perceived, priming effects in this paradigm cannot be attributed to conscious strategic processes that may take place after lexical access (for the prime) had occurred.

Since regions involved in motor preparation are under-activated in PD patients (Jahanshahi et al., 1995; Jenkins et al., 1992; Playford et al., 1992; Rascol et al., 1992, 1994), lexical access for masked verbs should be less efficient in PD if these regions really contribute to action word processing. Priming effects for action verbs, but not for concrete nouns, should therefore be reduced or even suppressed in PD patients off treatment. On treatment, however, no difference in priming effects between the two word classes should be observed, and PD patients should perform similarly to healthy controls.

2. Methods

2.1. Participants

Ten PD patients (six males and four females; mean age 62.8 years old ±8.7) and ten healthy control participants (six males and four females; mean age

Table 1
Characteristics of PD patients

Patients	Age (years)	Gender	Disease duration (years)	Dopa equivalence (mg/day)	UPDRS		DRS	BDI	Edinburgh Inventory
					OFF	ON			
PD1	57	F	14	1000	44	7	131	21	1
PD2	64	F	16	700	42	27	131	20	1
PD3	72	F	17	1300	29	14.5	137	28	0.9
PD4	55	M	7	700	38	15	136	13	0.9
PD5	65	M	7	1450	23.5	5.5	139	6	0.75
PD6	67	M	1	600	26	25.5	127	15	0.89
PD7	62	M	7	765	30.5	16	135	14	1
PD8	58	M	9	850	31.5	20	138	23	0.9
PD9	79	M	12	450	33	24	129	11	1
PD10	49	F	10	750	33.5	13	132	17	0.89
Mean (S.D.)	**62.8 (8.7)**		**10((4.8)**	**856.5 (311)**	**33.1 (6.6)**	**16.75 (7.4)**	**133.5 (4)**	**16.8 (6.4)**	**.92 (.07)**

Age, gender, disease duration, dopa equivalence and scores obtained for the different tests assessing motor disability (UPDRS Part III, maximal score = 108) during the OFF- and ON-phases, cognitive status (DRS, max = 144; BDI, max = 63) and laterality (Edinburgh Inventory, max = 1) are reported for each PD patient. Means (and standard deviations) are noted in bold in the last row of the table. M, male; F, female. Dopa equivalence: 100 mg dopa = 10 mg bromocriptine = 6 mg ropinirole = 1 mg pergolide = 1 mg pramipexole = 60 mg piribedil (see Thobois, 2006).

62.4 years old ±6.2), matched for age, gender, education and socio-economic status, participated in the study. All were French native speakers, had normal or corrected-to-normal vision, and were right-handed according to the Edinburgh Inventory (mean score: 0.92 at the Edinburgh Inventory, Oldfield, 1971; Table 1). None of the patients had a history of neurological or psychiatric disease other than PD. Control participants had no history of current or past neurological and psychiatric disease. All participants signed an informed consent prior to the experiment and were fully informed about the experimental procedure.

Patients fulfilled the UK Parkinson's Disease Brain Bank criteria for idiopathic PD (Gibb & Lees, 1988). They showed good responsiveness to Levodopa therapy and were hospitalized for medical check-up. They had been diagnosed between 1 and 17 years prior to their participation in this study. They performed the experiment twice in the same day: once off antiparkinsonian medication for at least 12 h (OFF-phase), and once 60 min after intake of a supraliminar dose of Levodopa (usual morning Levodopa-equivalent dose +25%; ON-phase; see Thobois, 2006 for Dopa equivalence). Motor disability was evaluated using the motor part III of the Unified Parkinson's Disease Rating Scale (UPDRS Part III, Fahn & Elton, 1987) in OFF- and ON-states. Cognitive performance was assessed using the Mattis Dementia Rating Scale (DRS; Schmidt et al., 1994) and the Beck Depression Inventory (BDI; Beck, Ward, Mendelson, Mock, & Erbaugh, 1961; Beck, 1979). Though slightly diminished, patients' DRS scores were in the normal range given their age. BDI scores also indicate that depression threshold was not reached. Scores obtained for the different tests are reported in Table 1.

2.2. Materials

2.2.1. Target stimuli

One hundred and forty words (70 action verbs and 70 concrete nouns) were selected from the French lexical database "Lexique" (New, Pallier, Ferrand, & Matos, 2001). Verbs, all in the infinitive form, denoted actions performed with the hand or the arm (e.g. draw), and nouns, in singular form, referred to imageable, concrete entities that cannot be manipulated (e.g. mill). Words that could be used as both nouns and verbs were excluded from the selection. Stimuli were matched for relevant lexical variables including word frequency, length in letters, number of syllables, bigram and trigram frequency and phonological complexity[1] (Table 2). Word age of acquisition was also controlled using empirical ratings performed by 15 volunteers on a seven-point scale (1 = [0–2

years] and 7 = [older than 13 years]; Gilhooly & Logie, 1980). Word imageability was estimated following the same procedure by another 15 volunteers (with 0 = impossible and 6 = very easy to generate a mental image of the word).

One hundred and forty pseudo-words, constructed by changing one letter from real nouns or real verbs, were added as fillers to perform the lexical decision task. Pseudo-words were thus either "pseudo-nouns" (70 items) or "pseudo-verbs" (70 items) and were all pronounceable. They were matched to words for relevant lexical variables (Table 2). Verbs and pseudo-verbs were also carefully matched for endings, such that as many verbs as pseudo-verbs (61/70 and 59/70, respectively) ended with "er", which is a frequent ending for verbs in French.

2.2.2. Prime stimuli

Primes consisted either of the same 140 words and 140 pseudo-words that served as targets, or of a group of 280 non-words (i.e. consonant strings not pronounceable in French; e.g., szmfr. Note that consonant strings served only as primes and never as targets). The total of 560 stimuli was divided in two equivalent experimental lists. In one list, half of the target words and pseudo-words was preceded (primed) by an identical prime (the same word and the same pseudo-word, respectively; we refer to this condition as identical-prime or repeated condition), while the other half was primed with a consonant string (we refer to this condition as consonants-prime or non-repeated condition). In the second list, target-prime relation was reversed. Thus, if in list 1 the target word "draw" was preceded by the prime "draw" and the target word "mill" was preceded by the consonant string "szmfr", in list 2, the target word "draw" was preceded by "szmfr" and the target word "mill" was preceded by "mill". Patients were tested with the same list in the OFF- and ON-phases.

In summary, pairs of prime/target could either be: (a) word/word (both words were identical), (b) consonants/word, (c) pseudo-word/pseudo-word (both pseudo-words were identical), and (d) consonants/pseudo-word. To minimize potential decision making strategies or response bias, the ratio between the number of target words and pseudo-words, as well as the ratio between identical-primes and consonants-primes was 1:1 (see Brown, McDonald, & Spicer, 1999; Brown et al., 2002; also Arnott & Chenery, 1999). Half of participants were tested with the first list and the other half with the second list. To ensure that priming effects were not simply due to visual summation of prime and target stimuli at a pre-lexical level (i.e. at the level of analysis of perceptual features of the words), prime stimuli were displayed in upper case while target stimuli were presented in lower case.

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[1] There is no lexical database for phonological complexity of French words. However, this variable is typically estimated from word length and from the structure of the constituting syllables, and defined as the sum of the complexity index of the syllables in a word (Paradis and Beland, 2002; Parisse and Maillart,

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2005). The complexity index is defined as follows: CV syllables have an index of: 1; V and CVC syllables: 1.5; CCV, CVV and CYV syllables: 2; CVCC syllables and other syllables: 2.5.

Table 2
Mean values (and standard deviations) of word frequency (FQ), length in letters (LETT), number of syllables (SYLL), bigram (BIGR) and trigram (TRIG) frequency, age-of-acquisition (AoA), imageability (IMAG), number of orthographic neighbours (ORTH NEIGH) and of phonological neighbours (PHON NEIGH), phonological complexity (PHON COMPL), and analyses of variance (ANOVAs) by items, for nouns, verbs and pseudo-words

	Nouns	Verbs	ANOVA (by items)	Pseudo-words	ANOVA (by items)
FQ	10.53 (32)	10.4 (30)	$[F(1,138) = .001; p = ns]$	–	–
LETT	6.57 (.94)	6.57 (.94)	*****	6.57 (.94)	*****
SYLL	2.11 (.55)	2.24 (.60)	$[F(1,138) = 1.737; p = ns]$	2.21 (.52)	$[F(1,278) = .190; p = ns]$
BIGR	4109(2348)	4676(2584)	$[F(1,138) = 1.842; p = ns]$	4379 (1960)	$[F(1,278) = .003; p = ns]$
TRIG	505 (434)	571 (621)	$[F(1,138) = .532; p = ns]$	472(443)	$[F(1,278) = 1.27; p = ns]$
AoA	4.38 (1.2)	4.11 (1.3)	$[F(1,138) = 1.556; p = ns]$	–	–
MAG	4.48 (.95)	4.22 (.70)	$[F(1,138) = 3.196; p = ns]$	–	–
ORTH NEIGH	1.74 (2.04)	3.54 (2.37)	$[F(1,138) = 23.056; p < .0001]$	–	–
PHON NEIGH	4.84 (5.38)	8.84 (6.41)	$[F(1,138) = 15.959; p < .0001]$	–	–
PHON COMPL	3.01 (.78)	2.98 (.76)	$[F(1,138) = .047; p = ns]$	–	–

ns, non significant. ***** No statistics were performed for this variable (number of letters) as it was equal for the two conditions (nouns and verbs = 6.57).

2.3. Procedure

Stimuli were displayed at the center of the screen of a PC monitor, using E-Prime software. As schematically indicated in Fig. 1, a display sequence started with a central fixation cross (500 ms), followed by a string of eight hash-marks (100 ms), the prime (50 ms), another string of hash-marks (100 ms) and the target stimulus. The target remained on the screen until participants indicated by a button press on one of two pre-selected keys on the computer keyboard, whether the stimulus was a word or not. Stimulus Onset Asynchrony (SOA; i.e. time interval between the onset of the prime and the onset of the target) was 150 ms. Participants were instructed to respond as quickly and as accurately as possible. For half of participants, response to words was given with the right hand and response to pseudo-words with the left hand. For the other half of participants, this relation was reversed. For a given patient, this response-setting was maintained in the OFF- and ON-phases. Recall that the critical comparison in this study is between the two classes of word stimuli (i.e. concrete nouns and action verbs) and not between words and pseudo-words. Response to both classes of words was always given with the same hand. Potential differences in performance for concrete nouns and action verbs can therefore not be attributed to response strategies due to the use of different hands—or to the fact that Parkinson's disease is an asymmetrical syndrome. Stimulus presentation was randomized and a training phase consisting of five words and five pseudo-words (different from the experimental stimuli) preceded the experiment. Subsequent to the experiment, participants were asked whether they had identified any primes.

Fig. 1. Experimental design. Grey boxes schematically indicate the different stimuli. Numerals plotted under each box denote corresponding display durations in milliseconds. The oblique axis on the right illustrates the temporal sequence of the stimuli and gives the onset of the corresponding item (time 0 corresponds to the onset of the fixation cross). Stimulus onset asynchrony (SOA, i.e. time interval between the onset of the prime and the onset of the target) is 150 ms.

2.4. Statistical analyses

Mean reaction times (in ms) were measured. Trials for which participants made an erroneous response and trials with reaction times below or above 2.5 standard deviations from individual means (a total of 2.64% trials for controls and 4.35% and 3.69% for patients in OFF and ON, respectively) were excluded from the analysis. Response latencies for nouns, verbs, pseudo-nouns and pseudo-verbs were first calculated individually and were then averaged over all participants. A first analysis of variance (ANOVA) with repeated measures with one factor ("Lexicality") allowed comparing performance for words and pseudo-words in healthy controls and in PD patients. This analysis served to verify whether patients performed the lexical decision task adequately. A subsequent ANOVA with repeated measures examined the effects of two main factors for the word stimuli only: "Word Category" (action verbs vs. concrete nouns) and "Prime" (identical-prime vs. consonants-prime). Significant interactions were assessed using one-tailed and two-tailed paired t-tests. In the same way, performance for PD patients in the OFF- and ON-phases were compared using an ANOVA with repeated measures with three factors (Phase – OFF vs. ON – Word Category and Prime), and paired t-tests allowed examining significant interactions. Finally, performance for controls and patients were compared using t-tests.

3. Results

None of the participants reported to have identified the primes.

In the following, results are first presented for control participants, and then for PD patients in the OFF- and ON-phases, respectively.

3.1. Control participants

The percentage of excluded "error" trials was $1\% \pm 1.91$ for nouns, $1.28\% \pm 1.72$ for verbs and $3.21\% \pm 3.09$ for pseudo-words.

Table 3a summarizes individual performance of the 10 control participants (C1–C10) in the two priming conditions for noun- and verb-stimuli. Net priming effects, which are the difference in response time for the consonants-prime condition and the identical-prime condition, are also given. Note that negative scores specify that reaction times were faster in the consonants-prime condition. Average performance with standard deviations is plotted at the bottom of the table. Except for participants C9 and C10, all participants were slower in the consonants- than
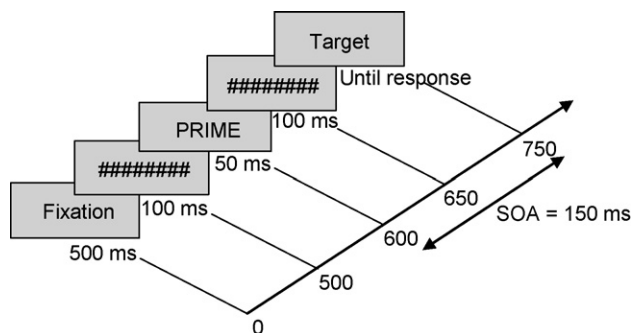
Table 3
Performance in the two priming conditions (consonants-prime and identical-prime) for nouns and verbs stimuli

(a)

Control	Nouns			Verbs		
	Consonants	Identical	Net priming	Consonants	Identical	Net priming
C1	688	633	**55**	593	536	**57**
C2	781	662	**119**	686	607	**79**
C3	734	696	**38**	712	672	**40**
C4	749	705	**44**	715	660	**55**
C5	736	712	**24**	726	683	**43**
C6	795	727	**68**	807	784	**23**
C7	826	741	**85**	837	774	**63**
C8	992	887	**105**	943	880	**63**
C9	1017	1045	**-28**	945	937	**8**
C10	998	997	**1**	1000	1031	**-31**
Mean	*832*	*781*	*51*	*796*	*756*	*40*
SD	*124*	*144*	*46*	*133*	*155*	*32*

(b)

PD off	Nouns			Verbs		
	Consonants	Identical	Net priming	Consonants	Identical	Net priming
PD1	971	890	**81**	967	950	**17**
PD2	1052	945	**107**	900	935	**-35**
PD3	786	735	**51**	797	770	**27**
PD4	1034	915	**119**	872	857	**15**
PD5	927	861	**66**	955	902	**53**
PD6	1080	1049	**31**	997	983	**14**
PD7	1292	1317	**-25**	1284	1263	**21**
PD8	1042	899	**143**	934	942	**-8**
PD9	833	783	**50**	827	792	**35**
PD10	1209	1021	**188**	1185	1261	**-76**
Mean	*1023*	*942*	*81*	*972*	*966*	*6*
SD	*155*	*163*	*61*	*153*	*171*	*37*

(c)

PD on	Nouns			Verbs		
	Consonants	Identical	Net priming	Consonants	Identical	Net priming
PD1	770	679	**91**	825	764	**61**
PD2	785	804	**-19**	716	728	**-12**
PD3	822	739	**83**	848	780	**68**
PD4	826	814	**12**	797	818	**-21**
PD5	874	912	**-38**	909	845	**64**
PD6	939	863	**76**	1046	922	**124**
PD7	1016	986	**30**	1109	1072	**37**
PD8	1154	1023	**131**	1043	1015	**28**
PD9	*	*	*	*	*	*
PD10	*	*	*	*	*	*
Mean	*898*	*853*	*46*	*912*	*868*	*44*
SD	*132*	*118*	*59*	*140*	*124*	*47*

Net priming effects are also given. Means and standard deviations (S.D.) are reported in italics in the two last rows of the table. Grey fields indicate negative priming effects (i.e. shorter reaction times in the consonants-prime than in the identical-prime condition). (a) For the ten control participants (C1–C10); (b) for the ten PD patients in the OFF-phase (PD1–PD10); (c) for the eight PD patients in the ON-phase (PD1–PD8; PD9 and PD10 could not perform the experiment in ON).

in the identical-prime condition. This indicates that the priming procedure was effective for the majority of participants.

A first ANOVA that tested the effect of "Lexicality" revealed the typical pattern in showing that mean reaction times were significantly longer to pseudo-words (1081 ms ± 283) than to words (791 ms ± 136; [$F(1, 9) = 25.79$; $p = .0007$]). The subsequent ANOVA that analyzed performance for word-stimuli only showed that the main factor "Word Category" had a marginally significant effect on performance ([$F(1, 9) = 4.08$; $p = .0742$; ns]), indicating slightly faster reaction times to verbs than to nouns. Such variations can occur when lexical factors are not entirely balanced between the two word classes. This

is not problematic, however, because we evaluate net priming effects, which compare performance for the same word class with itself (in the consonants- and identical-prime conditions). Mean reaction times to concrete nouns were 806 ms ± 132 and to action verbs 776 ms ± 144. The main factor "Prime" had a significant effect on performance ([$F(1, 9) = 15.29$; $p = .0036$]), with shorter mean reaction times in the identical-prime condition (768 ms ± 150) than in the consonants-prime condition (813 ms ± 126). Finally, no interaction between "Word Category" and "Prime" was obtained ([$F(1, 9) = 1.49$; $p = $ ns]), demonstrating that net priming effects were equivalent for action verbs (40 ms ± 32) and concrete nouns (51 ms ± 46). Reaction

times in the identical-prime condition were 756 ms ± 155 for verbs and 780 ± 144 for nouns. In the consonants-prime condition, they were 796 ms ± 133 and 832 ms ± 124, respectively.

3.2. PD patients

- OFF-phase:

The percentage of excluded "error" trials was 6.57% ± 6.69 for nouns, 2.71% ± 4.19 for verbs and 6.57% ± 4.58 for pseudo-words. Overall mean reaction times for PD patients in the OFF-phase (975 ms ± 157) were generally slower than for the control group (791 ms ± 137; $t(9) = 3.281$; $p < .0095$ two-tailed).

Table 3b plots the data of the ten PD patients in the OFF-phase. For concrete nouns, all but one participant (PD7) showed clear effects of priming. This indicates that the priming procedure was effective for PD patients as well. For action verbs, by contrast, no priming was observed for PD2, PD8 and PD10. Moreover, for the remaining six participants who showed priming in both conditions, smaller priming effects were observed for verbs than for nouns.

Like for control participants, the first ANOVA revealed a significant effect of "Lexicality", i.e. mean reaction times were longer for pseudo-words (1254 ms ± 327) than for words (975 ms ± 163; $[F(1, 9) = 11.06$; $p = .0089]$), testifying that PD patients performed the task adequately. The ANOVA that analyzed performance for word-stimuli showed no effect of "Word Category" ($[F(1, 9) = .042$; $p = ns]$), which indicates that patients responded to action verbs as rapidly as to concrete nouns (968 ms ± 161 vs. 982 ms ± 156, respectively). The factor "Prime" had a significant effect on performance ($[F(1, 9) = 41.32$; $p < .0001]$), with shorter mean reaction times in the identical-prime condition (953 ms ± 163) than in the consonants-prime condition (997 ms ± 152). However, in contrast to healthy participants, PD patients in the OFF-phase showed a significant interaction between "Word Category" and "Prime" ($[F(1, 9) = 6.71$; $p = .0291]$), demonstrating that net priming effects differed for concrete nouns and action verbs. Mean reaction times were actually shortened by 81 ms (±61) when a target noun was primed by an identical-prime (942 ms ± 163) rather than by a consonants-prime (1023 ms ± 155; $t(9) = 4.22$; $p = .001$, one-tailed; $p = .002$, two-tailed). For action verbs, no significant priming effect (6 ms ± 37) emerged (966 ms ± 171 for identical-primes vs. 972 ms ± 153 for consonants-primes; $t(9) = .533$; $p = .303$ one-tailed; $p = .607$ two-tailed).

A direct comparison of net priming effects between control participants and PD patients in the OFF-phase showed no difference for nouns ($t(18) = 1.249$; $p = .228$, two-tailed), but a clear significant difference for verbs ($t(18) = -2.403$; $p = .027$, two-tailed). Hence, while masked priming for concrete nouns had the same effect on response time for healthy controls and for PD patients, masked priming for action verbs was clearly less effective for PD patients than for controls.

- ON-phase:

Only 8 of the 10 PD patients performed the experiment during the ON-phase. Two patients could not participate because of severe dyskinesias.

The percentage of excluded "errors" trials was 4.1% ± 4.89 for nouns, 2.14% ± 2.25 for verbs and 7.95% ± 7.17 for pseudo-words. Overall mean reaction times for the eight PD patients during the ON-phase (883 ms ± 125) did not differ significantly from those of healthy controls (791 ms ± 137; $t(7) = 1.0556$; $p = ns$ two-tailed).

Table 3c plots individual data for each of the eight PD patients in the ON-phase. For concrete nouns and action verbs alike, all but two participants (PD2, PD5; and PD2, PD4, respectively) showed clear and comparable effects of priming.

Like in the OFF-phase, mean reaction times were significantly longer for pseudo-words (1190 ms ± 257) relative to words (883 ms ± 122; $[F(1, 7) = 18.34$; $p = .0036]$). No effect of "Word Category" was obtained ($[F(1, 7) = .410$; $p = ns]$), indicating that patients responded to action verbs in a comparable way than to concrete nouns (890 ms ± 130 vs. 875 ms ± 162, respectively). A significant effect of "Prime" was observed ($[F(1, 7) = 8.36$; $p = .0233]$), showing that patients recognized words faster when they were preceded by an identical-prime (860 ms ± 117) than by a consonants-prime (905 ms ± 132). However, contrary to the OFF-phase and similarly to performances of healthy participants, in the ON-phase, no interaction between "Word Category" and "Prime" emerged ($[F(1, 7) = .010$; $p = ns]$). In other words, priming effects in the ON-phase were equivalent for action verbs (44 ms ± 47; 868 ms ± 124 for identical-primes vs. 912 ms ± 140 for consonants-primes) and concrete nouns (46 ms ± 59; 852 ms ± 118 vs. 898 ms ± 132, respectively).

- Comparison of performance in the OFF- and ON-phases (with eight PD patients):

To directly compare performance in the two phases, we discarded the data from the two patients that could not be tested in the ON-phase.

A comparison of mean reaction times for words in the OFF- and ON-phases did not reveal any significant effect of "Phase" ($[F(1, 7) = 1.648$; $p = ns]$). No main effect of "Word Category" was observed ($[F(1, 7) = .2327$; $p = ns]$), but a main effect of "Prime" emerged ($[F(1, 7) = 27.571$; $p = .0012]$). The interaction between these three factors was also significant ($[F(1, 7) = 7.382$; $p = .0299]$), revealing the differential net priming effects for verbs, relative to nouns, in the OFF- and ON-phases. Paired t-tests revealed that net priming effects for verbs were as expected smaller in the OFF- (13 ms ± 26) than in the ON-phase (44 ms ± 47; $t(7) = -2.057$; $p = .039$, one-tailed; $p = .079$, two-tailed). A comparison of individual data in Table 3b and c shows that for all but one of the 8 PD patients (PD4), net priming increased between the two phases. By contrast, net priming effects for nouns did not differ systematically between the OFF- (72 ms ± 54) and ON-phases (46 ms ± 59; $t(7) = 1.051$; $p = .164$, one-tailed; $p = .328$, two-tailed).

Note also that UPDRS scores dropped considerably between the OFF- and ON-phases (Table 1). The difference between the two phases was highly significant ($[F(1, 7) = 21.217; p < .0002]$), which indicates that motor performance improved. However, simple regression analyses of individual UPDRS scores and priming effects in the lexical decision task did not reveal a systematic relation between the two measures. The limited number of participants and the large inter-individual variability of priming strength between participants in general may explain this result. That is, a patient with a relative low UPDRS score can have a smaller net priming effect than a patient with a relative high UPDRS score. Although net priming effects of both patients will increase with Levodopa intake, linear regression analysis will not necessarily capture this relation.

Finally, to verify whether patients' performance was modulated by variables such as the duration of the disease or their cognitive performance in general, we correlated the strength of

Fig. 2. Mean performance of the eight PD patients during the ON- and OFF-phases together with performance of the 10 healthy controls. Data are plotted for noun- (in white) and verb-stimuli (in black) as a function of priming conditions (consonants-prime and identical-prime). (*) Significant net priming effects (i.e. difference between reaction times in the identical-prime and the consonants-prime conditions); ns: non significant.

priming effects to these different variables. Although the duration of the symptoms of our PD patients was heterogeneous (between 1 and 17 years), a simple regression analysis showed that there was no significant correlation between this variable and priming effects for either nouns ($p = .59$ in the OFF-phase and $p = .92$ in the ON-phase) or verbs ($p = .65$ and .38, respectively). Similarly, no significant correlation was found between strength of priming and scores obtained at the different cognitive tests (DRS: nouns, $p = .74$ in OFF and $p = .78$ in ON, verbs, $p = .50$ in OFF and $p = .40$ in ON; BDI: nouns, $p = .56$ in OFF and $p = .07$ in ON, verbs, $p = .34$ in OFF and $p = .98$ in ON).

3.3. Control participants and PD patients during OFF- and ON-phases

Fig. 2 plots mean performance of the eight PD patients during the ON- and OFF-phases together with performance of healthy controls. Data are plotted for noun- and verb-stimuli as a function of priming conditions. As evident from this comparison, despite the fact that overall reaction times varied, significant priming effects were observed in all but one condition: action verbs in the OFF-phase of PD patients.

4. Discussion

The present study aimed at determining to what extent motor regions contribute to action word processing by comparing masked priming effects for action verbs and concrete nouns in non-demented PD patients off and on dopaminergic treatment. Our results reveal that processing of action words can be selectively disrupted following a pathology that affects the motor system. When PD patients were deprived of dopaminergic treatment, that is, when motor disability was strongest, masked priming effects for action words were nearly absent. At the same time however, robust priming effects were observed for concrete nouns, thus discarding the possibility that lack of priming for verbs was due to an overall decrease in the ability of PD patients to capture information from masked words. Interestingly, following Levodopa intake, priming effects for action verbs restored and appeared as strong as for concrete nouns, and comparable to those of healthy controls. Together with the results of the control group, this latter feature allows discarding the possibility that lexical features of the lists of action verbs and concrete nouns may have been responsible for the difference in priming strength between the two classes of words. For the same patients and using the same lists of words, priming effects were absent for action verbs but not for concrete nouns, and this only during the OFF-phase.

Hence, just like for motor preparation and execution (Dick et al., 1987; Haslinger et al., 2001), processing of action words in PD varies with treatment, which suggests that brain regions that are involved in motor processes are partly recruited during lexical access. Coherent with previous studies that showed deficits for verb processing in patients with progressive supranuclear palsy (Daniele et al., 1994) or motor neuron disease (Bak et al., 2001, 2006; Bak & Hodges, 2004), our results thus provide evidence that aspects of the meaning of action words could
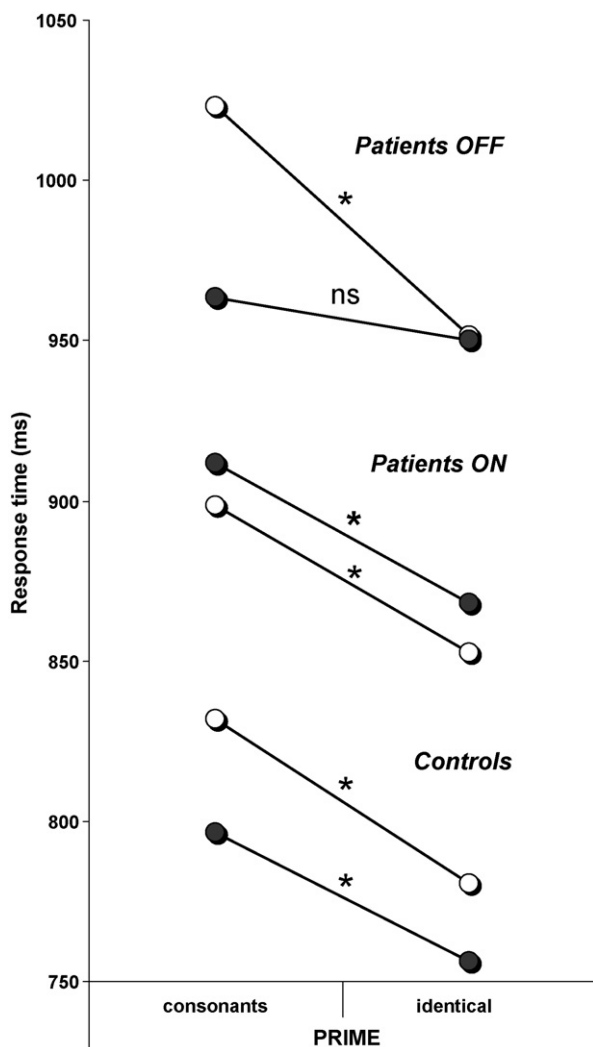
be represented in the motor system. However, since the dissociation between nouns and verbs in our study was only evident when priming effects were considered (but not when overall reaction times or error rates were measured), deficit in action word processing following motor impairments must be subtle. Other parts of the language network might therefore be sufficient to correctly identify these words. Note, though, that lack of priming for action verbs in our PD patients was obtained during the practically defined OFF-period, that is, while weaning was partial, temporary and minimal. The real impact of the motor system for processing action words might therefore have been underestimated. Note also that in as much as Parkinson's disease affects the nigrostriatal system (which projects to motor and premotor areas of the cortex), the present data document a nigrostriatal "modulation" of action word processing in motor areas. However, our results do not allow clearly identifying the locus of the identified word processing deficit. Although brain imaging studies point to the role of cortical motor regions in action word processing (Aziz-Zadeh et al., 2006; Hauk et al., 2004; Pulvermüller, Hauk et al., 2005), studies with patients suffering from lesions in motor and premotor areas are needed to clarify the precise role of the motor cortex in word recognition.

Previous studies have shown that non-demented PD patients can display deficits on more general measures of language functioning such as sentence comprehension (Grossman, 1999; Grossman et al., 1991; Grossman, Carvell, Stern, Gollomp, & Hurtig, 1992; Grossman et al., 2001; Lieberman, Friedman, & Feldman, 1990; Lieberman et al., 1992; Natsopoulos et al., 1991), language production (Beatty & Monson, 1989) or lexical ambiguity resolution (Copland, Chenery, & Murdoch, 2000). Verb learning (Grossman, Stern, Gollomp, Vernon, & Hurtig, 1994) and selective (oral) verb production deficits have also been reported (Bertella et al., 2002; Peran et al., 2003). While these language deficiency have classically been attributed to difficulties in processing grammatical information, especially about verbs, recent studies have suggested that they may rather reflect limitations of cognitive resources in terms of working memory or general slow down of information processing (Grossman et al., 2002; Grossman, Carvell, & Peltzer, 2005). Both interpretations, however, do not seem to account for the selective lack of priming effect for action verbs that we observed in our PD patients. First, masked priming is known to reflect automatic activation of lexico-semantic information at the word level (Ferrand et al., 1994; Forster & Davis, 1984; Greenwald, Draine, & Abrams, 1996). The deficit in action word processing of our PD patients may therefore occur at this particular level rather than at the grammatical level. Second, the fact that PD patients displayed normal priming effects for concrete nouns during the phase where no priming was observed for action verbs, is incompatible with the hypothesis that postulates a general slowing down of lexical retrieval for words in PD patients (Grossman et al., 2002). Similarly, accounts that relate deviant language processing in PD to a generalized alteration in neural signal-to-noise ratio (Angwin, Chenery, Copland, Murdoch, & Silburn, 2003; Bloxham, Dick, & Moore, 1987; Kischka et al., 1996; Spitzer & Neumann, 1996) – which could thus result in less efficient processing of weak signals such as masked words –

cannot explain the dissociation we found between action verbs and concrete nouns. In the same way, changes in the time-course of semantic activation observed in some PD patients as well as in healthy subjects who ingested Levodopa (Angwin et al., 2003; Angwin, Chenery, Copland, Murdoch, & Silburn, 2004; Angwin, Chenery, Copland, Arnott, et al., 2004; Arnott, Chenery, Murdoch, & Silburn, 2001) may not explain why priming effects in our study were absent only for action verbs in PD patients off treatment. Finally, for practical reasons, all PD patients performed the experiment first off and then on dopaminergic treatment. This could suggest that performance for action verbs improved in the ON-period because of learning. But here again, such learning bias cannot account for the dissociation between the two word categories, since performance for concrete nouns was comparable in the two phases.

According to our hypothesis, masked priming effects for action verbs are absent in PD patients because motor areas, which do not function adequately during dopamine depletion (Dick et al., 1987; Jahanshahi et al., 1995; Jenkins et al., 1992; Oishi et al., 1995; Playford et al., 1992; Rascol et al., 1992, 1994; Shibasaki et al., 1978), are involved in lexical access. This hypothesis joins recent theoretical arguments which consider language understanding either as a form of mental simulation involving the "mirror neuron system" (Gallese & Lakoff, 2005; Rizzolatti & Fadiga, 2004; Tettamanti et al., 2005), or as the result of Hebbian correlation learning between perisylvian language areas and motor regions (Pulvermüller, 2005). The mirror neuron system consists of visuomotor neurons, located in premotor and motor cortices, which respond to action execution, action observation and action-related sounds (Aziz-Zadeh, Maeda, Zaidel, Mazziotta, & Iacoboni, 2002; Aziz-Zadeh, Iacoboni, Zaidel, Wilson, & Mazziotta, 2004; Buccino et al., 2001; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Kohler et al., 2002; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Rizzolatti, Fadiga, Matelli et al., 1996). It has been suggested that mirror neurons code action content at an abstract level, accessible by language (Gallese & Lakoff, 2005). Hence, the meaning of action words could be assessed through the mirror neuron system by mentally simulating the described actions. The "Hebbian learning model", by contrast, postulates that meaning-related information about action words may be represented in motor areas (Pulvermüller, 1996, 2001, 2005), because functional links between cortical systems for language and action would develop during language acquisition (Pulvermüller, Shtyrov et al., 2005; Shtyrov, Hauk, & Pulvermüller, 2004). Any variable that affects the normal functioning of motor regions should thus affect the understanding of action-related language.

Whatever the exact underlying mechanism, the selective deficit for action verbs that we observed in the present study confirms previous suggestions that representations of concrete nouns and action verbs involve partly distinct brain regions (Boulenger, Decoppet, Roy, Paulignan, & Nazir, 2007; Caramazza & Hillis, 1991; Damasio & Tranel, 1993; Hillis, Wityk, Barker, & Caramazza, 2003), with the latter extending into motor areas (Aziz-Zadeh et al., 2006; Boulenger et al., 2006; Hauk et al., 2004; Oliveri et al., 2004; Pulvermüller, Shtyrov et

al., 2005; Shtyrov et al., 2004). The verb processing deficit in PD is mild though, which suggests that the contribution of motor regions to action word understanding may be relatively small. It is important to note here that human cortical motor regions seem to be involved in processing words describing human actions only, and are not recruited during processing of words describing actions performed by other species (Buccino et al., 2004; Mason, Banfield, & Macrae, 2004; see also Boulenger et al., 2007 for related findings). One possible contribution of motor regions to action word understanding could therefore be that of providing pragmatic knowledge about the actions described by the words.

In line with this speculation, neuropsychological studies have shown that focal brain disease or lesions can independently disrupt semantic and functional aspects of knowledge. Hence, patients with semantic dementia, for instance, can display degraded conceptual knowledge about objects (e.g. they fail to produce correct semantic descriptions about objects), while pertaining knowledge about how to use the objects appropriately (Buxbaum, Schwartz, & Carew, 1997; Hodges, Garrard, & Patterson, 1998; Lauro-Grotto, Piccini, & Shallice, 1997). Conversely, other patients are able to provide conceptual explanation about objects but fail to organize correct actions to and with these objects (De Renzi & Lucchelli, 1988; Ochipa, Rothi, & Heilman, 1989, 1992). Such dissociations have been taken as evidence that two independent subsystems – one for object semantics and one for action semantics – underlie representations of familiar objects. The results of the present study could thus suggest that action words are processed through separate pathways, one giving semantic information about the words (i.e. their meaning, the entities they relate to, in which context they are encountered, etc.), and the other providing prag-matic/functional information about how the actions they refer to can be performed.

In conclusion, the present study reveals that processing of action verbs can be selectively affected in PD patients off dopaminergic treatment, but that this deficit can recover following Levodopa intake. Although we still need to better understand the functional role of motor regions in action word understanding, our findings provide evidence that processing of action-related language partly relies on the motor system.

Acknowledgements

Appendix A

List of the words (concrete nouns and action verbs) used in the lexical decision task. Mean values of word frequency (FQ), length in letters (LETT), number of syllables (SYLL), bigram (BIGR) and trigram frequency (TRIG), age-of-acquisition (AoA) and imageability (IMAG), number of orthographic neighbours (ORTH NEIGH) and of phonological neighbours

Nouns	FQ	LETT	SYLL	BIGR	TRIG	AoA	IMAG	ORTH NEIGH	PHON NEIGH	PHON COMPL
Aigle	9	5	1	3627.42	194.03	3.28	5.32	7	3	1.5
Avion	34.71	5	2	3791.62	237.67	1.5	5.88	1	6	3.5
Canoë	1.29	5	3	4856.14	159.17	4.96	5.5	2	1	3.5
Hêtre	3.1	5	1	4917.89	1667.96	5.5	3.11	0	5	2.5
Hotte	1.77	5	1	4705.12	883.37	3.12	4.4	7	15	2.5
Hutte	4.13	5	1	4998.79	902.25	5.08	4.81	3	17	2.5
Panda	0.06	5	2	9829.56	490.58	3.32	5.77	4	13	2
Poney	0.39	5	2	9438.69	68.8	2.92	5.68	0	14	2
Ruche	1.97	5	1	1443.66	443.07	3.92	5.2	7	14	1.5
Totem	3.06	5	2	4508.98	201.47	5.4	3.86	0	0	2.5
Arcade	1.48	6	2	1355.19	117.82	5.8	3.5	2	2	4
Baobab	0.42	6	3	761.13	58.97	6	4	0	0	4
Cagibi	2.42	6	3	1423.11	33.53	5.48	3.54	0	0	3
Canyon	0.58	6	2	4775.36	98.74	6.12	3.36	1	11	3
Dindon	0.94	6	2	4158.66	43.2	4.08	5	3	2	2
Donjon	2.35	6	2	7228.84	704.43	4.56	4.95	1	3	2
Écluse	1.9	6	2	1672.2	184.56	5.4	3.27	3	2	4
Église	94.77	6	2	2345.58	237.43	2.93	5.5	0	0	4
Étoile	32.42	6	2	3838.43	227.65	1.45	5.61	2	0	4
Girafe	1.03	6	2	1567.74	84.21	2.32	5.86	0	0	2.5
Gradin	0.65	6	2	3693.58	679.36	4.96	4.81	2	5	3
Grotte	12.35	6	1	4013.74	424	3.05	4.55	5	9	2.5
Guenon	1	6	2	5105.99	167.03	3.95	3.9	0	5	2
Hangar	6.97	6	2	3741.31	277.73	5	4.59	0	5	3
Marais	9.65	6	2	8893.35	1445.96	5.73	3.2	8	30	2

Appendix A (*Continued*)

Nouns	FQ	LETT	SYLL	BIGR	TRIG	AoA	IMAG	ORTH NEIGH	PHON NEIGH	PHON COMPL
Moulin	14.52	6	2	11156.36	676.74	4	5.6	0	9	2
Mûrier	0.35	6	2	2879.87	288.44	6.4	3.81	2	4	3
Podium	0.58	6	2	3015.08	39.49	5.2	5	1	1	3.5
Ponton	1.1	6	2	10764.39	1702.65	5.07	3	2	11	2
Requin	1.29	6	2	3741.16	159.44	2.96	5.81	2	12	2
Toison	3.42	6	2	8015.57	1263.44	6.45	1.89	2	6	3
Virage	5.94	6	2	3063.64	336.67	3.76	5.09	7	7	2.5
Arbuste	1.32	7	2	1694.75	197.37	4.56	4.73	0	0	5
Auberge	9.71	7	2	3713.96	124.84	4.8	4.77	0	1	3.5
Bosquet	1.77	7	2	2248.54	599.46	6.32	3.5	1	3	2.5
Cabanon	0.9	7	3	2497.54	61.48	4.07	5	0	1	3
Calèche	2.29	7	2	4514.31	550.93	4.07	4.2	1	3	2.5
Caverne	4.9	7	2	2999.25	412.82	3.8	4.86	2	2	3.5
Chambre	231.23	7	1	3132.07	1005.93	1.35	4.72	2	6	2.5
Chameau	3.52	7	2	3897.52	1058.85	3.28	5.95	1	6	2
Cumulus	0.58	7	3	771.43	38.75	5.07	3.9	2	1	3.5
Éléphant	5.68	7	3	1570.36	457.78	2.12	5.86	0	2	3.5
Falaise	9.74	7	2	4701.2	798.53	4.15	4.39	3	5	2.5
Goéland	0.42	7	3	1242.53	110.42	4.8	4.5	0	0	3.5
Iceberg	0.77	7	2	1188.83	31.97	4.57	5.4	0	0	5
Licorne	1.1	7	2	2571.27	397.42	3.95	4.5	2	2	3.5
Oranger	1.61	7	3	4328.65	845.55	4.85	4.14	2	2	3.5
Oseraie	0.29	7	3	2658.04	311.02	6.8	2.2	2	7	3.5
Pommier	5.35	7	2	7236.32	1767.02	3.05	5.45	3	7	3
Prairie	9.29	7	2	6623.51	663.49	3.4	5.13	1	3	3
Sen tier	16.39	7	2	7737.99	1324.38	4.75	4.66	4	12	3
Tem pête	17.42	7	2	2971.79	562.34	4.07	2.8	2	3	2.5
Terrain	61.87	7	2	4704.97	969.53	3.7	3.61	3	14	2
Terrier	1.9	7	2	4955.02	1003.86	4	3.77	2	9	3
Tornade	1.9	7	2	3348.37	89.59	5.93	3.6	1	1	3
Tronçon	2.26	7	2	3593.77	617.72	6	3	0	3	3
Verglas	1.06	7	2	2519.03	322.98	5.07	4.2	0	0	3.5
Vitrine	11.42	7	2	4474.5	532.88	4.4	4.9	1	1	3.5
Bananier	0.45	8	3	4713.17	365.62	4.07	3	0	0	4
Banquise	1	8	2	3695.2	282.94	5.12	4.5	0	0	2.5
Barrière	12.48	8	2	4371.53	391.89	2.7	5.28	1	6	5
Bâtiment	19.26	8	3	2565.18	807.14	4.2	5	1	3	3
Cerisier	1.68	8	3	6076.53	479.05	4.04	5.54	1	1	4
Chevalet	3.35	8	3	2509.06	544.19	5.67	5	1	2	3
Corridor	5.06	8	3	5011.76	320.22	6.48	3.54	0	0	3.5
Grillage	5	8	2	1899.71	319.69	3.44	5.59	2	4	4.5
Monumen	8.61	8	3	6753.73	1246.29	5	3.5	0	0	3
Moquette	7.97	8	2	2650.77	339.62	3.12	4.81	7	8	2.5
Penderie	1.39	8	2	4693.45	765.49	5.44	4.68	0	4	3
Rambarde	1.32	8	2	1494.19	156.91	4.72	3.9	0	5	3.5
Mean	10.39	6.57	2.11	4109.40	505.37	4.38	4.48	1.74	4.84	3.01
Bâtir	8.13	5	2	1980.32	130.31	5.45	3.54	5	9	2.5
Cirer	1.68	5	2	4200.3	713.15	5.16	4.32	8	27	2
Jeter	38.77	5	2	6096.66	563.97	3.05	4.04	2	8	2
Ramer	0.97	5	2	3907.92	250.25	4.36	4.72	9	22	2
Râper	0.23	5	2	1759.06	99.85	4.88	4.22	3	26	2
Raser	4.03	5	2	5396.94	396.9432	4.0352	4.5	14	22	2
Saler	0.39	5	2	6306.76	471.06	3.68	4.45	7	25	2
Scier	2.39	5	1	2053.7	232.24	3.6	4.95	4	20	2
Semer	3.03	5	2	7081.73	399.07	5	4.18	1	7	2
Tâter	3.06	5	2	2869.17	476.8	4.88	3.18	5	26	2
Agiter	6.68	6	3	4791.1	466.91	3.76	4	3	10	3.5
Bêcher	0.58	6	2	2056.37	444.84	5.48	3.63	5	13	2
Border	1.19	6	2	4176.23	335.87	3.73	3.5	7	10	2.5
Broder	1.26	6	2	4120.21	224.72	5.56	4.18	7	9	3
Clouer	1.55	6	2	2785.02	112.47	4.15	4.45	4	6	3.5
Écrire	89.16	6	2	4081.88	472.55	2.07	5.8	4	3	4
Épiler	0.68	6	3	3463.74	210.76	6.04	4.45	3	6	3.5
Gommer	0.97	6	2	6779.04	3145.5	2.68	4.63	3	15	2

Appendix A (*Continued*)

Nouns	FQ	LETT	SYLL	BIGR	TRIG	AoA	IMAG	ORTH NEIGH	PHON NEIGH	PHON COMPL
Manier	5.97	6	2	7534.56	561.14	5.68	2.13	7	13	3
Masser	1.1	6	2	7792.34	1151.23	4.72	4	9	20	3
Moudre	0.74	6	1	11448.02	520.95	5.6	2.5	5	3	2.5
Opérer	12.06	6	3	3873.78	155.37	4.45	3.17	2	5	3.5
Palper	2.52	6	2	6251.71	79.96	6.2	3.04	4	6	2.5
Pétrir	1.9	6	2	3048.47	261.57	5.68	3.95	4	1	3.5
Pincer	2.35	6	2	3354.96	277.8	2.8	4.45	5	13	2
Racler	1.06	6	2	3989.2	227.73	5.84	3.32	3	8	3
Saisir	33.55	6	2	8440.48	2083.55	5.05	4.5	3	7	2.5
Serrer	13.42	6	2	8611.9	1106.28	4.7	3.6	5	14	2
Signer	9.23	6	2	3330.94	544.8	4.84	4.41	4	15	3
Tondre	0.77	6	1	9696.46	894.93	3.45	4.21	5	9	2.5
Tordre	2.9	6	1	5814.48	338.09	4.4	4.11	4	6	2.5
Vernir	0.39	6	2	3561.04	660.46	5.95	3.63	5	3	3
Agrafer	0.23	7	3	1835.31	68.29	4.4	5.4	2	5	4
Allumer	11.42	7	3	3168.82	462.47	2.55	4.23	2	7	3.5
Arroser	2.55	7	3	2497.37	412.32	2.8	4.81	3	7	3.5
Balayer	4.19	7	3	2455.48	246.47	3.12	5.04	2	3	4.5
Brosser	1.65	7	2	4158.96	599.1	2.07	4.8	4	8	3
Ciseler	0.23	7	2	3577.12	168.44	6.53	3.8	1	5	3
Creuser	7.61	7	2	3058.72	234.08	3.04	4.55	3	4	3
Enfouir	1.9	7	2	4528.46	371.87	5.8	2.6	3	2	3.5
Essuyer	6.03	7	3	3300.38	207.44	3.2	4.78	2	4	6
Faucher	2.06	7	2	3594.3	728.2	5.64	3.27	3	15	2
Ficeler	0.39	7	2	2829.61	131.14	5.04	4	1	4	3
Frapper	21.19	7	2	2929.02	354.41	2.85	4.5	2	7	3
Frotter	4.94	7	2	4005.42	424.38	3.25	4.06	6	13	3
Gratter	4.94	7	2	4152.75	744.68	2.7	4.36	2	9	3
Griffer	1.39	7	2	2372.61	141.21	2.6	4	3	11	3
Jongler	0.94	7	2	6503.16	289.8	3.84	5	2	2	3
Malaxer	0.19	7	3	4093.32	355.76	5.93	4.9	1	3	3.5
Mendier	1.81	7	2	4827.74	908.19	6	4.27	3	13	3
Montrer	66.61	7	2	10581.79	2856.44	2.7	4.17	3	8	3
Peigner	0.81	7	2	3148.86	288.22	3.07	5.4	2	8	3
Peindre	15	7	1	4426.16	475.79	2.7	5.2	7	10	2.5
Prendre	256.16	7	1	5136.04	955.6	2.05	4.12	1	0	2.5
Récurer	0.42	7	3	4612.62	484.71	6	4.8	1	4	3
Réparer	9.58	7	3	4701.41	736.26	3.65	3.5	3	6	3
Secouer	8	7	2	5271.19	540.37	4.1	4.18	2	5	3
Tapoter	0.87	7	3	2939.68	235.5	4.8	5	3	8	3
Astiquer	1.16	8	3	3880.11	594.07	5.4	3.37	1	4	4.5
Attraper	8.9	8	3	2471.49	391.91	2.36	4.2	2	5	4.5
Bricoler	0.97	8	3	2228.52	162.77	3.56	4	2	5	4
Caresser	9.32	8	3	5770.31	710.75	2.4	4.8	3	5	3
Colorier	0.32	8	3	5898.38	615.55	1.84	4.6	1	1	4
Déchirer	5.16	8	3	3705.59	572.54	3.04	4.23	2	6	3
Découper	3.81	8	3	3043.4	486.1	3.4	4.28	3	8	3
Dessiner	9.74	8	3	16644.66	3172.44	1.67	5.6	3	6	3
Pianoter	0.19	8	3	2788.21	149.2	5.06	4.5	0	3	4
Savonner	0.77	8	3	3341.17	403.38	3.47	4.72	1	5	3
Soulever	11.45	8	2	9276.43	1187.34	4	4	1	8	2.5
Tricoter	1.77	8	3	2900.61	193.54	3.72	4.9	3	5	4
Mean	10.53	6.57	2.24	4675.85	571.49	4.11	4.22	3.54	8.84	2.98

(PHON NEIGH), and phonological complexity (PHON COMPL) are reported.

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