

Action-verb processing in Parkinson's disease: new pathways for motor–language coupling

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Abstract Recent studies suggest that action-verb processing is particularly affected in early stage Parkinson's disease (PD), highlighting the potential role of subcortical areas in language processing and in the semantic integration of actions. However, this disorder-related language impairment is frequently unrecognized by clinicians and often remains untreated. Early detection of action-language processing deficits could be critical for diagnosing and developing treatment strategies for PD. In this article, we review how action-verb processing is affected in PD and propose a model in which multiple and parallel fronto-temporal circuits between the cortex and the basal ganglia provide the anatomic substrate for supporting action-language processing. We hypothesize that contextual coupling of action-language networks are partially dependent on cortical–subcortical integration, and not only on somatotopic motor cortical organization or in a mirror neuron system. This hypothesis is supported by both experimental and clinical evidence. Then, we identify further research

steps that would help to determine the reliability of action-language impairments as an early marker of PD. Finally, theoretical implications for clinical assessment and for models of action-language interaction (action–perception cycle theories, mirror system models of language, and embodied cognition approaches to language) are discussed.

Keywords Parkinson's disease · Action-verb processing · Basal ganglia · Motor–language coupling · Mirror neurons

Introduction

Parkinson's disease (PD) is a neurodegenerative disorder characterized by the loss of voluntary control over movement (Helmich et al. 2012; Liu et al. 2006; Rosin et al. 1997) caused primarily by a deficiency in nigrostriatal dopamine and subsequent functional impairment of the basal ganglia (BG) (Rodríguez-Oroz et al. 2009).

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Traditionally, early PD was defined as presenting only motor deficits, as the role of the BG in cognition was unknown. From the first descriptions of PD in the early nineteenth century until the last decades of the twentieth century, it was generally assumed that the language disturbances observed in PD were limited to changes in the motor aspects of language, characteristic only of the advanced stages of the disease (Cummings 1990). However, recent studies have highlighted the effects of PD on cognition, specifically on working memory (WM) and executive functions (EF), which are linked primarily to fronto-striatal circuits affected in PD (Dubois and Pillon 1997). In addition, speech and other language disturbances, as well as their neural correlates have also been reported in PD (Lieberman et al. 1992).

More importantly, early stage PD patients show deficits in action-word naming (Bertella et al. 2002; Cotelli et al. 2007; Peran et al. 2009), action-verb production (Crescentini et al. 2008; Peran et al. 2003), action-verb identification (Boulenger et al. 2008), and the contextual interaction between action-verb comprehension and motor response (Ibáñez et al. 2012). Several of these authors have suggested that the nigrostriatal circuit, affected in PD, is involved in modulating the processing of action-verbs in motor cortical areas.

Moreover, these findings on language impairments in PD may contribute to the current ongoing debate surrounding motor–language interaction theories (Hauk et al. 2004; Pulvermüller 2005; Pulvermüller and Fadiga 2010), the role of the mirror neuron system (Gallese and Lakoff 2005; D'Ausilio et al. 2009; Hickok 2010), and the involvement of the BG in language. Importantly, early identification of action-language processing deficits could play a crucial role in the diagnosis, treatment, and rehabilitation strategies for patients suffering from PD.

This article reviews neuropsychological and brain imaging reports that could shed light on our understanding of specific action-language dysfunctions associated with PD. Initially, we describe the main findings of changes in both the morphosyntactic and the lexical-semantic levels of the language domain associated with PD. In the next section, we review published works on the action-verb processing deficits observed in early PD and critically assess the interaction between subcortical and cortical areas in terms of motor and language functions. Finally, we propose a model of motor–language coupling underlying action-verb impairments in PD, discuss the theoretical and clinical implications and provide suggestions for further research.

General language impairments in PD

Language deficits in individuals suffering from PD have now been extensively reported in the literature (Cummings

et al. 1988). Studies derived from simple picture tasks (Arnott et al. 2005), together with data from functional imaging (Grossman et al. 2003), suggest that PD can affect most aspects of language comprehension and production (Fig. 1). Morphosyntactic processing, lexical-semantic processing, and discourse level processing have all been shown to be affected in individuals with PD (Table 1).

Parkinson's disease patients have been shown to have problems with comprehension of complex sentence structures (Angwin et al. 2006). Surprisingly, early stages of morphosyntactic processing remain relatively intact in PD (Friederici et al. 2003a; Longworth et al. 2005) (Fig. 2).

Morphosyntactic deficits observed in PD have been attributed to EF deficits. Underlying deficits in WM, which is required to understand complex sentences, may explain language impairments (Hochstadt et al. 2006; Longworth et al. 2005). Morphosyntactic comprehension deficits have been regarded as an epiphenomenon of deficits in other cognitive functions, such as selective attention (Lee et al. 2003) and executive resources (Angwin et al. 2006; Hochstadt et al. 2006). In terms of language production, individuals with PD appear to have morphosyntactic impairments regardless of the presence or absence of dementia (Longworth et al. 2005; Terzi et al. 2005).

Deficits in lexical semantic processing in PD have been shown to appear both in production and comprehension. Copland (2003) suggests that lexical semantic deficits in comprehension are caused by disinhibition, i.e., an inability to properly choose between competing interpretations of a given stimulus. Discourse comprehension impairments in PD include understanding implied and metaphorical meanings and also integrating information (Berg et al. 2003; Monetta and Pell 2007). One study found that there are only weak correlations between performance in discourse comprehension and aphasia subtests (Murray and Stout 1999). This finding would suggest that deficits in this area are, again, not language-specific, but rather a result of the general cognitive deterioration in PD, in particular WM, which is essential for the integration of old and new information (Monetta and Pell 2007; Murray and Stout 1999). Morphosyntactic comprehension and semantic processing studies are summarized in Table 2.

Overall, PD patients display a variety of deficits in morphosyntactic, lexical-semantic, and discourse-level processing. It remains to be determined whether these deficits are caused by a language-specific impairment, more general deficits in EF, or a specific decline in WM.

Action-verb processing in PD

The study of action-verb processing in PD has been shown to be a relevant area of study for two main reasons. First, deficits in action-verb processing may be a cognitive

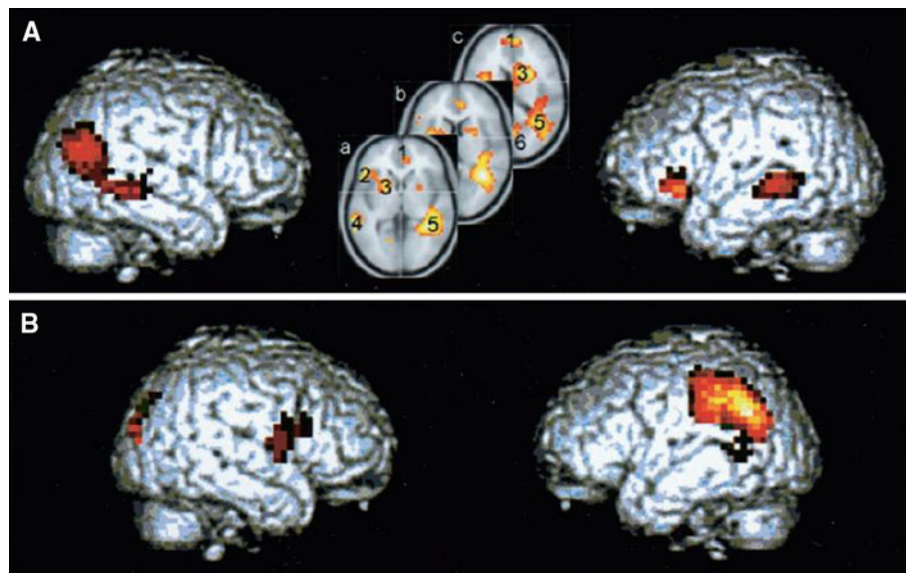


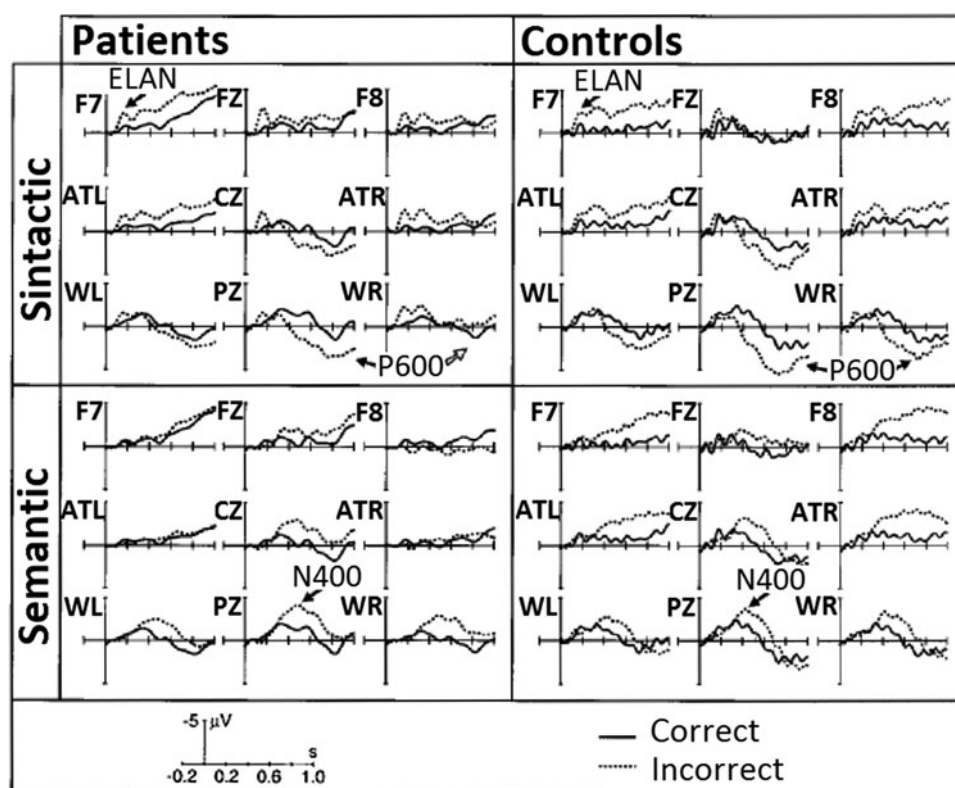
Fig. 1 Regional activation patterns in direct contrasts of PD patients and healthy seniors. **A** Areas of reduced activation in PD patients relative to healthy seniors for object-relative long-linkage sentences, including lateral views and representative transaxial views (left hemisphere on the left) at $z = 0$ mm (a), $z = +8$ mm (b), and $z = +16$ mm (c). 1 Bilateral anteromedial prefrontal, 2 left ventral inferior frontal, 3 bilateral striatum, 4 left posterolateral temporal, 5

right posterolateral temporal, 6 bilateral occipital. **B** Areas of increased activation in PD patients relative to healthy seniors for object-relative long-linkage sentences. PD patients showed less striatal activation when processing long sentences and less bilateral fronto-temporal activation. Reprinted from Grossman et al. (2003), with permission from AAN Enterprises, Inc.

Table 1 Summary of morphosyntactic comprehension studies in PD

References	Participants (mean age)	Medication	Task	Biomarker	Main findings
Morphosyntactic comprehension					
Angwin et al. (2006)	20 PD patients without dementia (64 years), 23 healthy controls	Levodopa (18) Cabergoline (7) No medication (1)	1. Self-paced reading task (24 sentences) 2. Auditory comprehension test (36 sentences)	None	Slowed sentence processing and comprehension in PD
Arnott et al. (2005)	19 non-demented patients with PD (61 years), 19 healthy controls	Levodopa	On-line word recognition tasks	None	PDs could activate morphosyntactic information in an automatic manner but the information is available for a short time. Brief activation leads to poor integration
Hochstadt et al. (2006).	45 PD patients without dementia (66 years)	No specific	1. Reading span test of verbal WM 2. Sentence–picture matching test of meaning from syntax (TMS)	None	Difficulty on sentences with complex syntax comprehension in mild and moderate PD
Grossman et al. (2003)	7 non demented PD patients (71 years), 9 healthy controls	No specific	Sentence comprehension task	fMRI	PD patients showed less striatal activation when processing long sentences and less bilateral fronto-temporal activation
Zanini et al. (2004)	12 bilingual PD patients (58 years), 12 healthy controls	Levodopa and dopaminergic antagonists	Sentence comprehension and sentence judgment	None	Worse performance of PD participants in the L1 than in the L2
Lee et al. (2003)	19 PD patients (68 years), 15 controls in one task, 16 controls in the other one	Uncontrolled	Sentence comprehension, and word detection	None	Limited executive resources for attention and processing speed contribute to deficits in sentence comprehension in PD

Fig. 2 Average event-related brain potentials for the syntactic and semantic conditions at selected electrode sites. The *solid line* represents the correct sentence condition; the *dotted line* represents the incorrect sentence conditions. The *vertical lines* indicate the onset of the critical word. *ELAN* early left anterior negativity. The semantically related ERP (N400) was present in both groups. In the syntactic domain, late integrational processes (P600) were affected in PD. Reprinted from Friederici et al. (2003a, b), with permission from American Psychological Association, Inc



marker of early PD in the absence of any other cognitive deficits. Second, this language impairment makes it possible to connect clinical aspects of PD with neurocognitive models of motor–language coupling. As mentioned above, studies have shown that the motor system plays a fundamental role in action-verb comprehension/production (Pulvermüller 2005; Pulvermüller and Fadiga 2010). Fronto-striatal connections (Booth et al. 2007) and the BG may also be involved in the interaction between language and motor systems. In the following paragraphs, we review the main findings on verb processing in PD (Table 3 summarizes the literature).

Using a picture-naming task with 102 figures (52 objects and 50 actions), Bertella et al. (2002) showed that early stage PD patients had specific difficulty generating action-verbs. Participants (22 PD patients and 20 controls) free of basic cognitive impairments, as confirmed by the Mini Mental State Examination (MMSE) and Raven's progressive matrices, performed a naming task. Early PD patients performed worse than controls, but they were relatively more impaired in action naming than in object naming. The authors argue against the idea that actions are simply more cognitively demanding, given that in Alzheimer's disease (AD), object naming has been found to be more compromised than action naming (Cappa et al. 1998). However, this study had a number of limitations (e.g., no report of anti-parkinsonian medication and phase; absence of multivariate correlations with the neuropsychological profile).

Peran et al. (2003) studied 34 early PD patients tested in the “on” medication phase and 34 matched controls using a word generation test. Cognitive performance was assessed using the MMSE and the Dementia Rating Scale (DRS). Motor disability in PD patients was evaluated using the motor part of the Unified Parkinson's Disease Rating Scale (UPDRS). The experimental paradigm contained 80 stimuli (40 nouns and 40 action-verbs) divided into two intracategorical (verb/verb and noun/noun) and two intercategory (verb/noun and noun/verb) blocks. The experiment involved listening to each word and then producing an associated noun or verb, a task designed to be relatively easy, thus lowering the cognitive load in terms of EF such as WM and planning. Results showed that relative to controls, PD patients showed poorer verb processing performance, producing a greater number of grammatical errors in all tasks involving verbs. Multivariate analysis showed a negative correlation between memory subscore (DRS) and intercategory block (i.e., noun/verb). However, no correlation was found between error rate and motor scores (UPDRS) or any other measure. The authors suggest that prefrontal cortex dysfunction underlies these language impairments (Bak et al. 2001; Cappa et al. 1998). Moreover, noun processing, which is apparently preserved in PD, has been associated with the left inferior temporal lobe (Shapiro et al. 2006).

Cotelli et al. (2007) studied picture-naming in 32 early PD patients and 15 healthy subjects. The two types of pictures they used were matched for lexical frequency and

Table 2 Summary of morphosyntactic production and semantic processing studies in PD

References	Participants (mean age)	Medication	Task	Biomarker	Main findings
Morphosyntactic production					
Terzi et al. (2005)	27 PD patients (64 years), 27 healthy controls	Antiparkinsonian	Past tense processing	None	No specific language deficit. Poor performance due to cognitive demands
Longworth et al. (2005)	7 patients with subcortical ACV; 15 PD and 10 Huntington patients (54 years)	Levodopa and dopamine agonists	Elicitation and priming of past tense	None	Automatic activation spared, inhibition disrupted
Lieberman et al. (1992)	20 mild (61 years) and 20 moderate PD (69 years); 40 Controls	Uncontrolled	Sentence comprehension and voice onset time (VOT) measures	None	Comprehension errors, VOT disruptions
Syntactic and semantic processing					
Friederici et al. (2003a, b)	8 PD patients and 8 age-matched controls (57 years)	Levodopa Phase ON	Auditory sentence processing of semantic congruency and syntactic violations	ERPs	The semantically related ERP (N400) was present in both groups. In the syntactic domain, late integrational processes (P600) were affected in PD
Copland (2003)	10 Parkinson's disease (PD) (69 years), 10 nonthalamic subcortical (NS), 10 vascular lesions, 10 cortical lesions, and 10 matched controls	Levodopa Unspecific phase	Semantic priming task	None	Basal ganglia dysfunction interrupts the attention engagement of the semantic network assessing meaning frequency
Demakis et al. (2003)	25 PD patients after unilateral pallidotomy (64 years)	Levodopa Phase ON	Fluency test (COWAT)	None	Decline on verbal fluency due to decreased general cognitive functioning
Berg et al. (2003)	30 PD patients (67 years), 26 controls	Levodopa Unspecific phase	Battery of tests: repetition and recreating sentences, inferences, comprehension, definitions	None	Poor performance in detecting implied meaning
Monetta and Pell (2007)	17 patients and 17 controls (66 years)	Levodopa and dopamine agonists	Metaphor comprehension task	None	Poor performance is due to verbal working memory deficits

length. Action pictures and object pictures were separated into two sub-categories, one which involved fine hand movements and the other one which did not. All patients were on antiparkinsonian medication at the time of testing. Neuropsychological assessment included measures of general cognitive functioning (MMSE and Raven's progressive matrices), construction ability (Rey-Osterrieth complex figure), verbal tasks (standard verbal fluency paradigm and history recall), and basic EF (Trail Making Test A and B). Early PD patients showed a general deficit in both action naming and object naming. Furthermore, only the PD group performed worse on action naming, with respect to object-naming. Finally, the authors reported a significant negative correlation between each patient's action naming impairment and his/her score on a visual memory task, which suggests that the visual complexity of the drawings could have influenced the ability to name action pictures. The authors suggest that action naming

deficit in PD could be caused by the disrupted functioning of prefrontal areas, due to PD induced subcortical–prefrontal disturbances.

Crescentini et al. (2008) evaluated noun and verb generation with a method similar to the one used by Peran et al. (2003) in non-demented PD patients. Twenty early PD patients (during the “on” phase of levodopa or a dopamine agonist) and 20 controls, matched for age, gender, education, and MMSE scores were evaluated. Motor disability was evaluated using the UPDRS. The experiment contained 27 nouns for both generation tasks (noun/verb and noun/noun). In addition, stimuli pair association was determined by close probability scores condensed in three conditions. As expected, relative to controls, PD participants exhibited verb-generation deficits, which were mostly grammatical in nature. In contrast, patients were comparable to controls in the noun-generation task. Moreover, in the PD group, verb-generation deficits

Table 3 Summary of action-verb processing studies in PD patients

Author	Participants (mean age)	Medication	Task	Biomarker	Main findings
Nouns vs. action-verbs					
Bertella et al. (2002)	22 early PD patients and 20 healthy controls (64 years)	No specific	52 pictures of objects and 50 pictures of actions to be orally named	None	A noun/verb dissociation with a relative verb deficit was found in patients affected by PD
Peran et al. (2003)	34 early PD patients (63 years) phase on and 34 healthy controls	Levodopa (29) Dopamine agonists (5)	Noun and verb generation (40 concrete nouns and 40 action verbs)	None	PD specific verb-generation task deficits in and similar performance than controls in a noun-generation task
Cotelli et al. (2007)	32 early PD patients phase on (69 years) and 15 healthy controls	Levodopa (32)	(60) Action/(60) object picture naming task	None	Deficit in object and action naming, especially in action naming in PD
Crescentini et al. (2008)	20 early PD patients (65 years) phase on and 20 healthy controls	Levodopa (16) Dopamine agonists (17)	Noun and verb generation task (noun–verb, 27/noun–noun, 27 stimuli)	None	PD presented general deficits in noun and verb generation and remarkable impairments in verb category
Boulenger et al. (2008)	10 non-demented PD patients (62 years) phase off and on and 10 healthy controls	Levodopa (10)	Priming paradigm 140 words (70 action-verbs/70 concrete nouns) 140 pseudo-words 280 non-words	None	Dopaminergic treatment selectively influences the RT of action-word processing of concrete nouns during lexical decision in PD
Rodriguez-Ferreiro et al. (2009)	28 PD non-demented PD patients (75 years) 28 AD patients and healthy controls	No specific	50 object pictures and 50 action pictures	None	Significant PD impairments to name actions compared to objects
Peran et al. (2009)	14 non demented PD patients (64 years), phase “on”	Antiparkinsonian medication	A set of object drawing was used: (1) Object naming (2) Generation of verb denoting an action that could be performed with object depicted	fMRI	Preferential involvement of the prefrontal cortex, Broca’s area and anterior cingulate cortex for action-verb generation in PD
Fernandino et al. (2012)	20 non demented PD patients (64 years), 17 phase on, 3 off, and 22 healthy controls	Levodopa	80 verbs and 80 phonologically legal pseudowords	None	Relative to healthy controls, PD patients were more impaired on action verbs than abstract verbs processing.
Herrera and Cuetos (2012)	20 early PD patients (60 years) phase on and off, and 20 healthy controls	Levodopa	4 verbal fluency tasks: phonological, semantic and action	None	Compared to controls, PD (off medication) produced fewer words in all categories. Regarding frequency, differences were found between PD patients and controls for the action-word category
Ibáñez et al. (2012)	17 early PD (62 years) phase on and 15 healthy controls	Antiparkinsonian medication	Action-sentence compatibility effect (ACE) paradigm and kissing and dancing test (KDT)	None	PD patients with preserved general cognitive repertoire showed a much diminished ACE and KDT deficits relative to controls

correlated with several neuropsychological EF scores. However, no correlations were observed between the error rate in verb production and UPDRS motor scores. As verb-generation deficits tend to be highly correlated with executive dysfunction in early PD patients, the authors

concluded that the language impairment in early PD was likely due to underlying neural mechanisms responsible for selecting and inhibiting responses.

Boulenger et al. (2008) studied noun and action-verb processing in 10 non-demented PD patients and 10

matched controls using a priming paradigm. They tested patients' lexical decision latencies for nouns and verbs while "on" versus "off" L-DOPA. Stimuli included 140 words (70 action-verbs representing hand or leg movements and 70 concrete nouns, which were imaginable but not manipulable), and 140 pronounceable pseudo-words derived from real words. These stimuli were used as either targets or primes. In addition, 280 non-words were used only as primes. Compared to control participants, who presented priming effects for the two kinds of words, PD patients did not show a priming effect for verbs during the "off"-phase. More importantly, following L-DOPA intake, patients displayed a recovery of priming effects for action verbs and performed similarly to the control group on the concrete nouns category. These results indicate that processing of action verbs can be selectively affected in non-demented PD patients when the effect of L-DOPA wears off and that performance can improve during the "on" phase of medication.

Rodriguez-Ferreiro et al. (2009) studied 28 non-demented PD patients, 28 AD patients, and controls. General cognitive function was determined using the MMSE. On the MMSE, the AD patients scored the lowest, and the PD group performed similarly to control participants. In the experiment, the stimuli included 50 object-pictures and 50 action-pictures (matched on several psycholinguistic variables), which were presented in two separate tasks. Participants were instructed to describe each picture using a single word that was either a noun or the infinitive form of a verb. The overall performance of the control group was higher than that of AD or PD patients. Interestingly, only PD patients showed a significant impairment in action naming compared to object naming.

Peran et al. (2009) used fMRI during the generation of action-verbs in 14 right-handed non-demented PD patients

("on" phase). Absence of cognitive impairment was determined by the MMSE. Motor disability was assessed with UPDRS motor score. They used 50 manipulable-object pictures (25 man-made objects and 25 manipulable biological objects). Stimuli were presented in two randomized blocks. In the first block, participants were asked to name object drawings aloud. Then, in a subsequent block, subjects had to orally produce a verb denoting an action that could be performed with the object depicted. Performance on these tests clearly indicated that non-demented PD patients made more errors in action-verb generation than in object naming. There was no correlation between action naming deficits and motor impairment (UPDRS). Neuroimaging data revealed involvement of an extended cortical network during action-verb generation. Furthermore, neural activity was observed in the left inferior and superior parietal cortex (Fig. 3). In addition, when they used a more permissive statistical threshold, they found a preferential involvement of the prefrontal cortex, Broca's area, and anterior cingulate cortex for action-verb generation. Moreover, a positive correlation was found between UPDRS score and brain activity during generation of action-verbs in the pre- and post-central gyrus bilaterally, left frontal operculum, left supplementary motor area, and right superior temporal cortex (Fig. 4). These results indicate that the frontal cortex may play an important role in action-verb generation tasks. Alternatively, they suggest that an impairment of motor striatal-frontal loops in PD patients may result in the recruitment of a cortical network designed to alleviate the deficit in these loops during the demanding action-verb generation task.

Fernandino et al. (2012) evaluated the processing of action and abstract verbs in 20 PD patients and 20 healthy controls without cognitive impairment (MMSE ≥ 24). To examine the effect of task demands, the authors used two

Fig. 3 Activation maps ($p < 0.05$ at cluster level) in manipulable biological objects (blue); or man-made objects (orange). **a** Object naming (ON), **b** generation of action-verbs (GenA). Reprinted from Peran et al. (2009), with permission from Elsevier

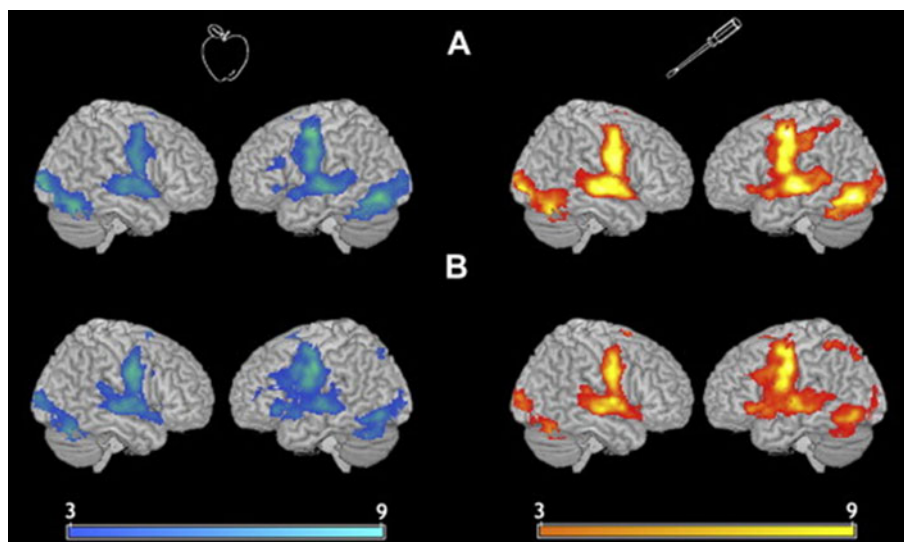
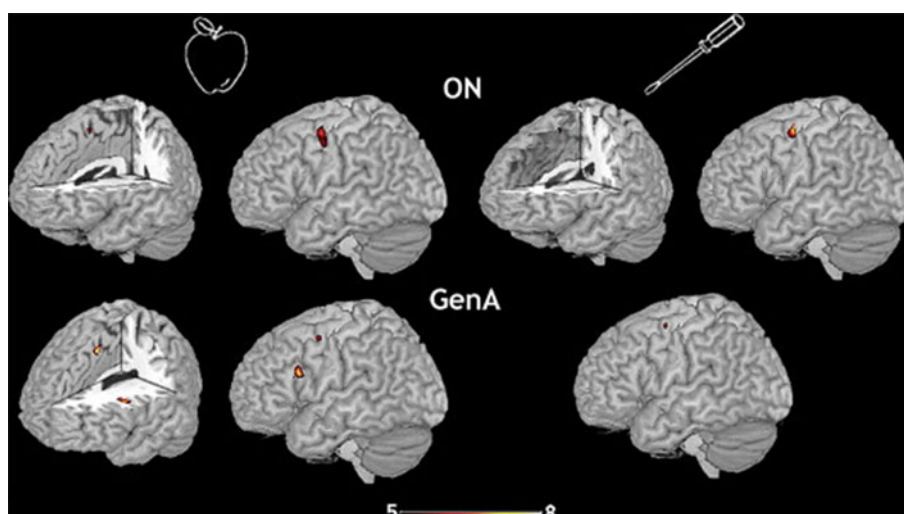


Fig. 4 Activation maps of positive correlations between each condition and the motor deficit ($p < 0.001$ uncorrected). Reprinted from Peran et al. (2009), with permission from Elsevier



different experiments in which the semantic demands were either implicit (lexical decision and priming) or explicit (semantic similarity judgment). The lexical decision task contained 80 verbs and 80 phonologically legal pseudo-words. Half of the verbs referred to voluntary hand/arm actions (e.g., to grasp, to squeeze), and the others referred to abstract concepts (e.g., to depend, to improve). Relevant linguistic variables were matched between lists. The semantic similarity judgment task contained 240 stimuli (120 action verbs and 120 abstract verbs). Each set was organized into 40 triplets, such that in each triplet, two of the verbs had similar meanings. The two conditions were matched for relevant linguistic variables. As expected, relative to controls, PD patients performance was selectively impaired for action verbs in both tasks, indicating that the motor system plays a more central role in the processing of action verbs than in the processing of abstract verbs.

Herrera and Cuetos (2012) studied verbal fluency in 20 non-demented PD patients while “on” versus “off” L-DOPA, and 20 healthy controls. General cognitive function was determined using the MMSE. The authors used four different verbal fluency categories: phonological (words beginning by *F*), semantic (animals and supermarket items), and action fluency (infinitive form of verbs, “things you can do”). Results showed that compared to control subjects, PD patients with “on” and “off” medication exhibited word generation deficits in phonological, animal and action categories. PD patients during the off phase have access to high frequency verbs only, while their performance when dopamine was restored was similar to controls. The present study provides further evidence of a specific deficit in PD patients during off medication in phonological and actions categories while these differences were restored with dopamine treatment. The authors suggest that dopamine plays a role within the lexico-semantic system particularly for retrieving verbs.

Finally, in a recent study, Ibáñez et al. (2012) used the action-sentence compatibility effect (ACE) paradigm in 17 early PD patients (during the “on” phase of levodopa or a dopamine agonist) and 15 controls, matched for age, gender, education, and handedness. Motor disability was evaluated using the UPDRS. All subjects in the study, both early PD patients and controls, scored within normal limits on the Addenbrooke’s cognitive examination revised (Torralva et al. 2011) and the INECO frontal screening (Torralva et al. 2009).

The ACE task required participants to listen to sentences describing actions typically performed with an open hand (e.g., clapping), a closed hand (e.g., hammering), or neutral (no hand action., e.g., visited); and to press a large button with either an open- or closed-hand position immediately upon comprehending each sentence. The ACE is defined as a longer reaction time (RT) for incompatible action sentences, relative to compatible action sentences. Early PD participants, with preserved general motor and cognitive repertoire, showed a much diminished ACE relative to non-EPD volunteers (Fig. 5a, b). These results could not be explained by general cognitive deficits or impaired EF. Moreover, a strong correlation between ACE performance and measures of action verb processing was observed (Fig. 5c). This study showed that action-verb deficits precede the onset of executive dysfunction in PD.

The same authors (Ibáñez et al. 2012) reported the ACE paradigm with direct recordings of primary motor (M1), premotor (PMC) cortices and semantic (left inferior frontal gyrus (IFG) and middle/superior temporal gyrus) areas (with electrocorticography, ECoG) in epileptic patients. Motor preparation affected language processing areas, and language processing affected activity in movement related areas (Fig. 5d–g). Thus, this study provided simultaneous evidence for (a) bidirectional motor–language cortical coupling and (b) direct influence of subcortical impairments (BG) on this coupling.

In brief, the findings reviewed above (summarized in Table 3) provide evidence that PD patients display consistent impairments in action-word processing. In this way, BG would also play an important role in motor–language integration. Noun or object processing most likely involves more posterior brain regions, and the processing of action-related language partly relies on the motor system. Although the data presented here suggest a strong link between motor actions and semantic processing of verbs, this relationship seems to be bidirectional. Instead of a single causal model supporting a topographic motor cortex foundation for language, this paper proposes the existence of a relatively nonspecific relationship between motor preprocessing (probably including M1, PMC, BG as well as other areas) and language. Moreover, this relationship seems to exist both at the cortical and subcortical levels of processing.

The clinical relevance of action-verb processing in PD

Given that the deficits in cognitive functions are an important cause of functional impairment in PD, there has been emerging interest in identifying a specific cognitive profile predictive of incident dementia in PD, for devising appropriate intervention techniques. In this preliminary review, we suggest that action-verb processing could be used like a potential cognitive marker of early PD. However, there are several necessary key points to establish the viability of this hypothesis in a putative fashion.

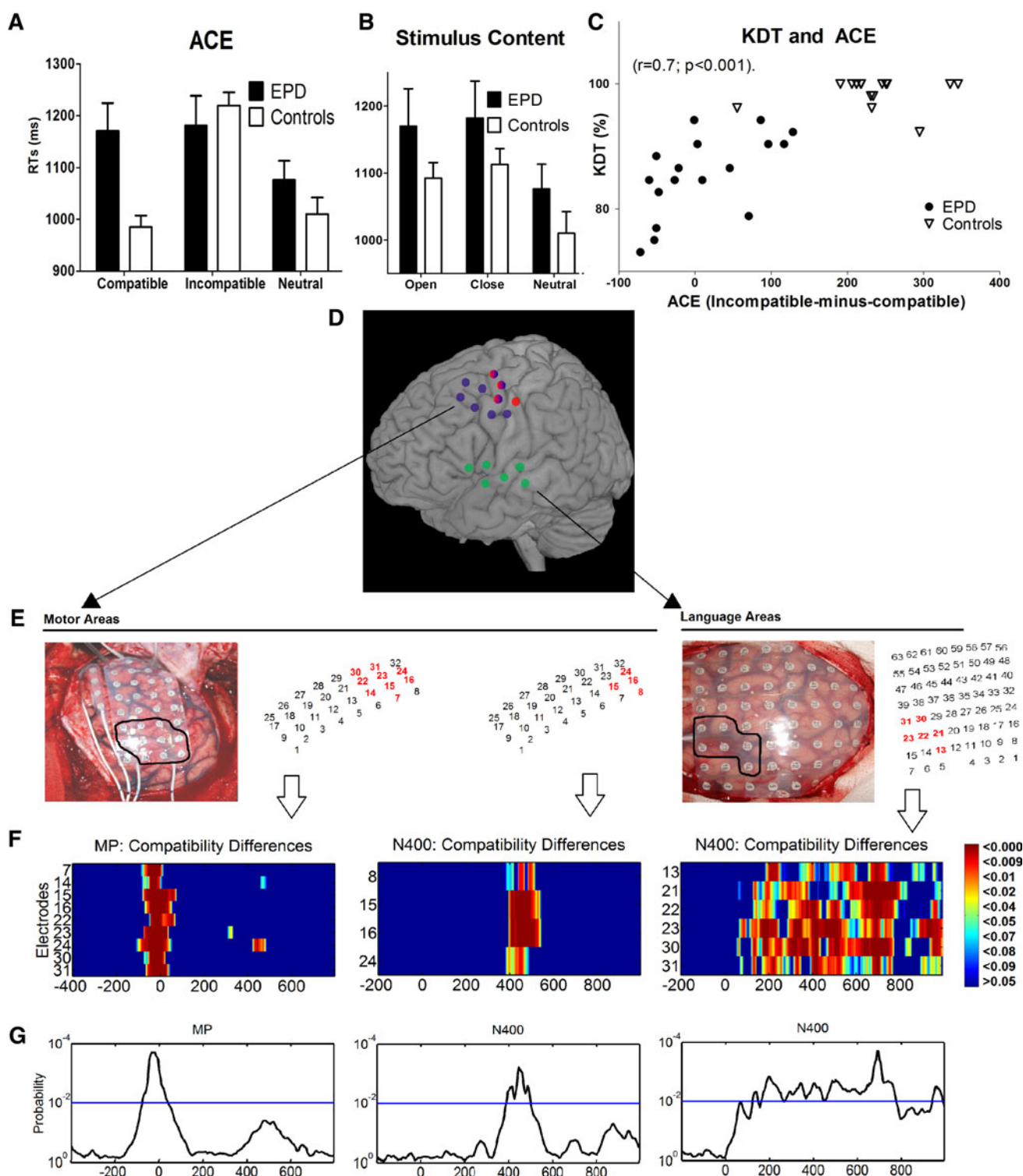
First, growing evidence suggests that action-verbs processing impairments during early stages of PD would be a specific marker of the disease. However, this deficit may not be exclusive to PD but extended to other neurodegenerative diseases. For instance, progressive supranuclear palsy is associated with selective impairment in verb processing (Bak et al. 2001, 2006), frontotemporal dementia shows a similar pattern (d'Honinchtun and Pillon 2008; Rhee et al. 2001), and verb-processing deficits have been reported in Amyotrophic Lateral Sclerosis (Bak and Hodges 2004; Neary et al. 2000). It should be noted that this evidence is supported by naming tasks, which do not provide a direct measure of participants' motor actions. The use of ACE paradigms (or similar, given the involvement of current motor responses linked to action-verbs) would help identify the degree of specificity of motor–language impairments in PD with respect to other neurodegenerative conditions. In addition, further experimental and neuroimaging studies in patients with motor system diseases might help both to identify more acutely the specific cognitive profile (e.g., characteristics of action-language impairment) and to determine the shared and distinct neural components that belong to language and motor simulation of actions. Thus, the comparison of motor diseases is a required step to determine the specificity of action-language impairments in PD.

Second, the evaluation of action-language impairments during PD sub-clinical stages would help determine if this deficit is present even before other domains are affected. For instance, the assessment of the genetic familiar PD version (e.g., homozygote PARK8 mutation), during the prodromal or subclinical phase of the disease would be very helpful for this purpose. This approach will allow to test if action-verb processing impairments are present before the clinical and cognitive manifestation of the disease.

Third, another way to prove the action-verb processing as a marker of PD patients consists in comparing not only the global performance of PD groups regarding controls, but also the individual PD performance. At present, findings in this language domain are referred to global results of PD patients. Others have proposed that early markers of PD, such as executive dysfunction (Lewis et al. 2003; McKinlay et al. 2010; Woods and Troster 2003) are also reported at group and not yet at individual level. Further studies should index reliability of potential cognitive markers (action-language deficit, executive dysfunction) at individual level.

Fourth, and related to this last issue, the primary or secondary manifestation of early action-verb deficits in PD remains unclear and should be directly investigated in further studies. Crescentini et al. (2008) argued that PD language impairment is due to executive dysfunction rather than to a primary linguistic disorder. Several reports (Lewis et al. 2003; Muslimovic et al. 2005; Woods and Troster 2003) have suggested that deficits in EF (including planning, WM, verbal fluency and attention) appear to constitute the core deficits for early PD. Impairments in these cognitive domains are thought to reflect fronto-striatal dysfunction caused by nigrostriatal dopaminergic depletion. Nevertheless, recent findings have shown that the precise underlying anatomical and neurochemical basis responsible for EF impairments in PD, involves a large dynamic range of neurotransmitters/neurochemical levels (for a review, see Calabresi et al. 2006). Moreover, there is evidence showing that early PD patients with reasonably intact executive functions present this language related disorder (Ibáñez et al. 2012). In the same line, Fernandino et al. (2012) have shown that action-verb impairments in PD seems to place a lower demand than other abstract processing on executive functioning. Nevertheless, this evidence is preliminary and further research is necessary to determine if action-verb processing is a *sui generis* affection in EPD.

Fifth, action-language assessment would offer potential new avenues to develop effective rehabilitation and stimulation programs. The longitudinal assessment of action-verb processing, together with clinical assessment in PD patients may provide further insights as well as



intervention strategies that may be effective in delaying the cognitive decline. In support of this suggestion, executive dysfunction can be successfully reduced through cognitive training in PD (Sammer et al. 2006), and this training is effective in compensatory reinforcement for functional decline (Sinforiani et al. 2004). Currently, the potential

effect of cognitive stimulation programs in motor–language interactions has not been tested. This is an interesting and novel possibility for rehabilitation strategies.

The further development of the above summarized five steps would help determine the reliability of action–language impairments as an early marker of PD. At present,

◀ **Fig. 5** ACE in early PD and ECoG. **a** Mean RTs from compatible, incompatible and neutral trials for PD and CG participants. CG participants show a classic ACE (compatible facilitation and incompatible delay of RTs), whereas the ACE was absent for EPD participants. **b** Preserved motor response discrimination for EPD participants. In both groups, OH and CH sentences produce longer RTs than neutral sentences due to a higher frequency and higher cloze probability of neutral sentences (Aravena et al. 2010). **c** Verbal processing (KDT) is associated with the ACE. The ACE is computed as the subtraction between incompatible and compatible trials (the higher the time interval, the stronger the ACE). KDT scale denotes percentage of correct responses. In **a** and **b** the bars depict the SD. **d** Motor and language areas producing an ACE. Normalized position of the electrodes showing a significant ACE (compatibility effect) superimposed in a render 3D map of the canonical CH2bet from MRIcron software. The figure depicts the position of electrodes evincing an ACE from both patients' grids in a common space showing the activation of IFG, STG and MTG (language-related areas) and the MFG, PM and M1 (motor-related areas). Electrode color is indicative of iERP modulation: MP (blue); M-N400 (Red); L-400 (green). **e** Pictures of subdural grids and electrode arrays. In the three schematic grids, numbers in red are indicative of significant compatibility effects observed at those sites for MP, M-N400 and L-N400 (from left to right). **f** Time-probability charts showing the significant effects at MP in premotor/motor (M1, ventral and dorsal PM) areas and N400 windows (M-N400 localized in premotor/motor areas including M1 and ventral–dorsal PM area; and a L-N400 localized in STG, MTG and inferior frontal gyrus). **g** Point-by-point *p* value waveform of the compatibility effect for MP, M-N400, and L-N400. The blue lines highlights the $p < 0.01$ threshold. Modified from Ibáñez et al. (2012)

we propose a hypothetical distinct BG role associated with a more extended frontotemporal network involved in the early phase of action-verb processing (see below), being partially independent of executive demands. This cortical–subcortical pathway may presumably underlie language–motor integration.

Hidden function of the BG in action language

The role of BG in higher-order cognitive functions remains unclear. Traditionally, the BG have been considered a secondary component of the motor system (Penfield and Rasmussen 1950; Penfield and Boldrey 1958). Classical BG models propose a unitary and exclusively motor function. Early attempts to explain the role of the BG assumed that these nuclei only play a role in slow movement (DeLong 1971, 1973; Kornhuber 1971) and the selection and inhibition of competing motor programs (Mink and Thach 1993; Vitek and Giroux 2000). Recently, non-motor functions such as reward processing (Yin and Knowlton 2006; Antzoulatos and Miller 2011) have been evidenced. In addition, BG are now thought to be crucial in the acquisition of implicit learning and habit formation (Yin and Knowlton 2006; Knowlton et al. 1996).

Furthermore, several authors highlight the potential participation of BG in the integration of complex domains of language and cognition. Houk (2005) argued for the BG

modulation of cortical patterns of activation for embodied action and thoughts and suggested a direct involvement of BG in language processing. Subcortical aspects of language have received limited attention. Only recently, cortical–subcortical interactions, in the context of distributed networks, have been systematically considered with regard to language function and semantic integration.

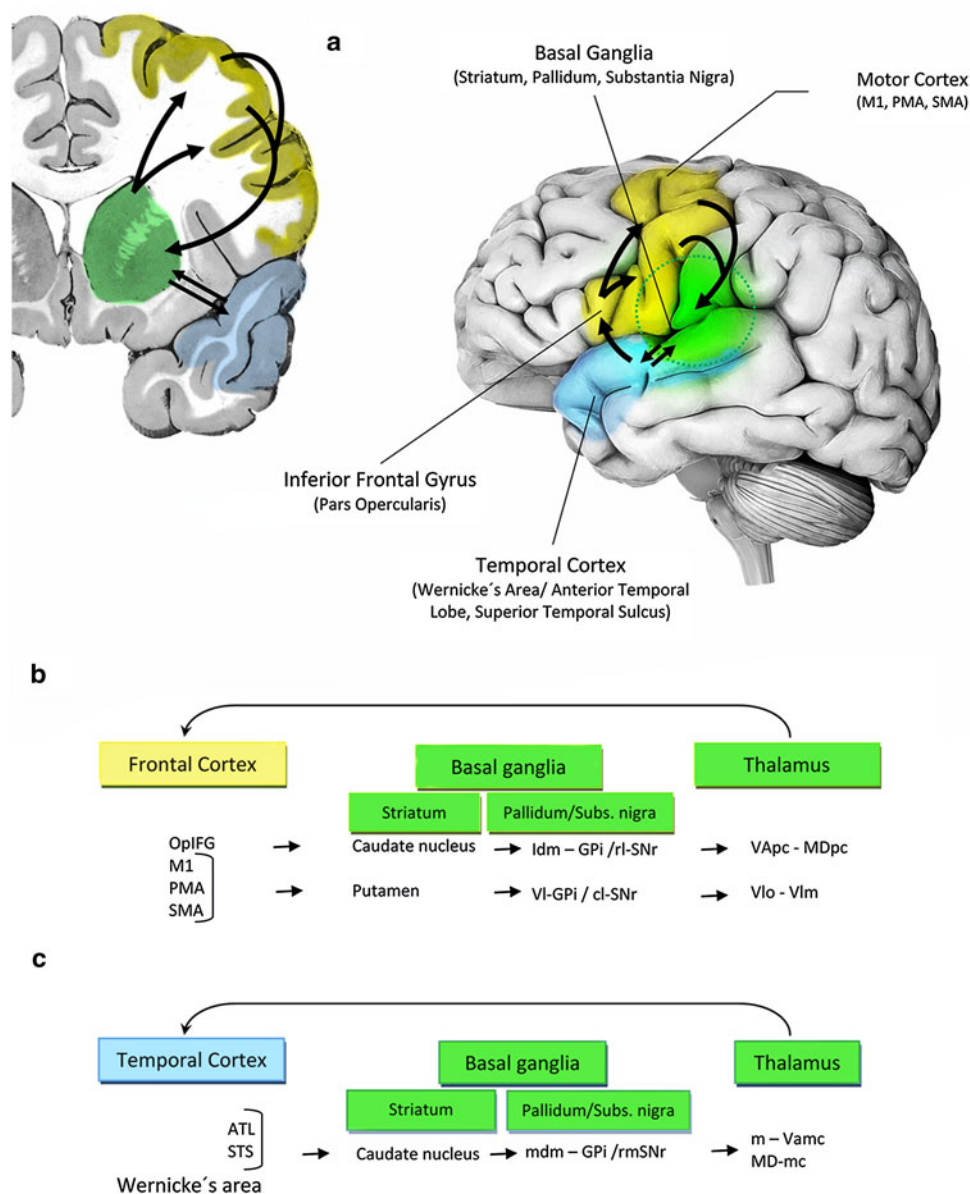
The involvement of the BG in language has received increasing attention (Booth et al. 2007), especially regarding syntactic processing (Friederici et al. 1999; Friederici 2002; Hagoort 1993; Longworth et al. 2005; Kotz et al. 2009). Recent brain imaging studies support this BG function (Friederici et al. 2003a, b; Moro et al. 2001). Moreover, studies of frontostriatal networks have highlighted the role of the BG in semantic processing. Current reports (Kotz et al. 2009) have provided additional support for this view by demonstrating that BG–thalamocortical circuit would be active in the integration of semantic and syntactic information.

The BG have profuse connections with the cerebral cortex, particularly with the frontal lobes (Middleton and Strick 2000, 2002; Ullman 2006). These networks seem to participate in movement control and higher cognitive functions. BG activation during semantic tasks (Abdullaev and Melnichuk 1997; Copland 2003; Crosson et al. 2003) suggests that this region together with M1 and prefrontal areas operate in parallel to integrate motor–semantic information. The critical role of BG in motor control, acquisition of habits, and action generation, has led to the suggestion that BG–thalamocortical loop would be involved in neural mechanisms that support the initiation of both semantic integration and motor representation presumably underlying action/verb processing.

A bidirectional model of motor–language coupling

Here, we propose a hypothetical model of motor–language coupling to understand the specific action–language impairments in early PD (Fig. 6). The proposal here is that hypothetical distinct BG–thalamocortical circuitry may modulate the motor–language integration observed in action/verb processing. It does this through the loops of interaction that project from cortical areas to BG to thalamus and back to cortex. The core assumption is that BG language network may include two major subcomponents (motor and semantic circuits).

The first component (frontal areas) includes the pars opercularis of the inferior frontal gyrus (OpIFG), M1, PMC, and supplementary motor (SMA) areas. We hypothesize that this circuit would be involved in the processing of motor simulation and action patterns in cortical areas. This activity would be mediated by the BG related with the automatic selection of motor activation and



pre-established action programs that are processed by cortical regions. Connectivity studies of these areas have shown relevant participation in language processing (Eickhoff et al. 2009).

The second component (temporal areas) would play a major role on the ground of abstract conceptual knowledge. The implicit learning and simulation of action generation indexed by the BG may modulate and directly influence the semantic processing in temporal areas such as the anterior temporal lobe (ATL) and superior temporal sulcus (STS). Recent accounts have proposed the existence, in ATL, of a mechanism supporting the interactive activation of semantic process across modalities (Patterson et al. 2007). Additionally, studies have consistently demonstrated that STS (including Wernicke's area) is seen as a prime area for

speech (Shultz et al. 2012; Mottonen et al. 2006). In addition, direct connections between frontal lobe (IFG) and ATL have been evidenced with monkey anatomical tracer data (Nelissen et al. 2011) and human DTI data (Saur et al. 2008). These connections allow for direct access to conceptual or semantic knowledge in anterior temporal cortex from frontal regions.

Thus, in this model the BG would influence both (a) frontal and (b) temporal processing of action verbs: (a) the BG action generation of learned actions/motor skills would prime the frontal simulation of intrinsic action meaning of verbs; and (b) the BG activation (together with frontal regions) would provide the grounding of motor experiences to be further processed as more abstract or conceptual relations at temporal sites. This BG role would

◀ **Fig. 6** Hypothetical schematic representation of major cerebral circuits underpinning action-verb processing that is disrupted in Parkinson's disease. **a** Coronal and lateral view of the left hemisphere showing the proposed frontotemporal basal ganglia–thalamocortical network (light yellow, blue, and green regions of interest, respectively). The arrows on the figure indicate the suggested principal flow of information involved in the action/verb processing through two main overlap sub-circuits. **b** Frontal–basal ganglia–thalamocortical component. The frontal lobe, basal ganglia and thalamus comprise loops which would integrate the motor simulation and action programming. The pars opercularis of inferior frontal gyrus (OpIFG) has a key role motor simulation (Pobric and Hamilton 2006). Accordingly, OpIFG project to caudate nucleus, which is involved in complex cognitive processes (Grahn et al. 2008). Medium spiny neurons in this region in turn converge onto the lateral dorsomedial globus pallidus (internal segment, Ldm-GPi) and the rostromedial substantia nigra pars reticulata (rl-SNr) from which pathways diverge to the ventral anterior (VA) and medial dorsal (MD) thalamic nuclei (Middleton and Strick 2000). These neurons project back to the frontal cortex. In the same way, frontal motor regions including: primary motor (M1), premotor (PMA) and supplementary motor (SMA) areas, contribute to motor programming and execution. Additionally, we suggest that these cortical regions play a complementary role in action/verb processing. These areas are differentially connected to the putamen which appears to subserve habit learning (Pobric and Hamilton 2006). Neurons of putamen project to ventrolateral globus pallidus (internal segment, VI-GPi) and the caudolateral substantia nigra pars reticulata (cl-SNr) from which pathways diverge to ventrolateral nucleus of thalamus pars oralis (Vlo) and ventrolateral nucleus of thalamus pars medialis (Vlm), and hence to specific cortical regions, primarily in frontal cortex. **c** Temporal–basal ganglia–thalamocortical component. The temporal lobe, basal ganglia and thalamus comprise hypothetical loops that would play a central role on the ground of abstract conceptual knowledge involved in words referring to motor concepts. The ATL would be directly related with semantic processing (Patterson et al. 2007) and the superior temporal sulcus (STS) (including Wernicke's area) is seen as a crucial region for the neural speech representations (Shultz et al. 2012; Mottonen et al. 2006). Cortical areas, ATL and STS project to caudate nucleus from which pathways diverge to dorsomedial globus pallidus (internal segment, mdm-GPi) and rostromedial substantia nigra pars reticulata (rm-SNr). This hypothetical circuit projects primarily to medial ventral anterior nucleus of thalamus pars magnocellularis (m-Vamc), and magnocellular subnucleus of mediodorsal nucleus of the thalamus (MD-mc) (Middleton and Strick 1996). These output structures (m-Vamc and MD-mc) also project back to ATL and STS areas

be part of a more general frontotemporal network engaged in the prediction of the meaning of the event, based on the integration of contextual cues and learning from previous experiences (Amoruso et al. 2011, 2012; Couto et al. 2012; Ibañez and Manes 2012). Certainly, this is a preliminary and hypothetical model that can be evaluated by further research. In the following paragraphs, some evidence from different domains supporting these hypothetical considerations is provided.

One major assumption of our model is that action/verb processing depends on BG–thalamocortical circuitry, which projects to specific frontal areas including PMC, sensorimotor cortex as well as pars opercularis (BA 44) of the left IFG. These frontal regions have been associated with both

motor planning and execution (Grezes and Decety 2001; Pobric and Hamilton 2006), but also with action observation (Tremblay and Small 2011). More importantly, direct involvement of those areas in verbal processing has been observed (Pulvermüller 2005; Pulvermüller and Fadiga 2010). There is converging evidence that supports the existence of cortico-BG–thalamocortical circuitry that projects to frontal regions. Anatomical findings in non-human primates (Antzoulatos and Miller 2011; Lo and Wang 2006; Pasupathy and Miller 2005; Middleton and Strick 2000, 2002) and functional neuroimaging studies in humans (McNab and Klingberg 2008; Booth et al. 2007; Lehericy et al. 2004), confirm a large-scale network of interconnected frontal regions (as well as to temporal) and the BG. The potential role of BG in action-verb processing would be related to the simulated action generation of predetermined motor patterns contained in the verbal descriptions of movements, leading to the automatic pre-activation of action simulation in frontal areas.

Basal ganglia functionality in PD would also underlie the acquisition of implicit learning affecting action and cognition. Non-declarative motor habits comprise a sequence of movements that subsequently become automatic. The habit formation system of the BG appears to be specialized for gradual learning and experience (Yin and Knowlton 2006; Knowlton et al. 1996). In this sense, the involvement of nigrostriatal pathway in PD is linked with slowness in the initiation of voluntary movement and the loss of automaticity of motor programs underlying BG function (Helmich et al. 2012; Liu et al. 2006; Rosin et al. 1997).

Additionally, implicit learning and automatic task performance are impaired in PD patients (Yin and Knowlton 2006; Knowlton et al. 1996). This presumably occurs because there is a lack of dopaminergic activity within the nigrostriatum pathway. Thus, the loss of automatic action generation in PD would disrupt the semantic grounding of motor experiences, triggering specific action/verb impairments.

Thus, clinical and experimental evidence lead us to propose a preliminary model in which frontotemporal parallel circuit interactions with BG provide the anatomic substrate for supporting not only motor execution, but also action-language processing. Language disturbance would occur at an early stage of PD, when cognitive functions are still relatively preserved, and therefore, EF deficits may only partially explain the specific verb processing impairment. BG impairment, along with relatively preserved fronto-striatal circuits, could be responsible for action-language impairments in early PD. EF, on the other hand, may play a complementary and incremental role on language deficits at later stages of the disorder. The neurocognitive model of motor–language coupling should be considered hypothetical, as a proposal to be adjusted and/or

reconsidered with further research. We consider this model as the first step in an attempt to develop a more comprehensive functional profile of cortical–subcortical action language underlying PD.

Relevance of BG findings for theories of action-perception cycle, mirror neuron system, and embodied semantics

Embodied cognition

The embodied cognition approaches propose that the human mind is largely determined by the ecological coupling of sensorimotor systems, emotions, and the current environment. Related theories (action-perception cycle, mirror systems, and embodied semantics) provide specific considerations about the role of experience. In this section, we compare these theories taking into account the revised evidence about the involvement of BG in action language.

The fundamental scheme of perception–action cycle assumes a circular flow of information from the environment to sensory and motor structures. The discovery of mirror neurons, responding both to action execution and observation, suggested an embodied approach to mental simulation (Buccino et al. 2001; Gallese and Lakoff 2005). According to this idea, the perception–action mechanism could be extended to several sensory and high level cognitive modalities such as emotion processing and empathy (Decety and Grèzes 2006). These accounts of sensory-motor coupling are in agreement with theories of embodied cognition, which suggest that cognitive representations are essentially grounded in bodily states and in the brain's modality-specific systems (Gallese and Sinigaglia 2011; Gallese and Lakoff 2005). Thus, “understanding” is sensory and motor simulation. In other words, a radical embodied view suggests the existence of a conceptual or symbolic interface that would consist of the sensory and motor knowledge (Mahon and Caramazza 2008). According to this view, Fernandino and Iacoboni (2010) proposed that concepts must be grounded on sensorimotor experience in order to have meaning. In this sense, this neural system may underlie human capacity to perceive, not only the actions, but also the sensations and emotions of others (Gallese 2001; Gallese et al. 2004; Rizzolatti and Sinigaglia 2010).

Embodied cognition, mirror neuron system, and language

In a similar vein, MNS theory states that the neuroanatomic substrate of action execution (i.e., sensorimotor system) are also recruited during action observation, planning, and mental imagery (Rizzolatti and Craighero 2004; Rizzolatti

and Luppino 2001; Rizzolatti et al. 2001; Gallese et al. 1996). A related embodied semantic hypothesis suggested that processing/comprehension of action/verbs may also recruit those sensorimotor regions (Kemmerer and Gonzalez-Castillo 2010; Gallese and Lakoff 2005; Pulvermüller 2005). These theories have also granted an important role to Broca's area in the semantic representation of actions (Rossi et al. 2011) because this cortical area seems to be important for both language processing and motor execution. As is the case of action-perception theories, mirror neuron-related approaches suggest a crucial role of cortical motor areas in action-language understanding (Glenberg et al. 2008).

However, there are a number of considerations which suggest the inadequacy of a causal hypothesis of MNS as the unique basis for action-language processing.

For example, Arbib (2010) suggested that besides mirror neurons located in the IFG (including Broca's area), different brain regions are involved in language processing, including prefrontal cortex and temporal areas. In a similar vein, Arevalo et al. (2012) argue that a number of areas in M1 and PMC, including mirror neuron regions, as well as additional areas in frontal and temporal cortex, play a complementary rather than a central role in processing words referring to motor related concepts.

Another critical consideration is that the evidence thus far only suggests that the MNS may participate in and enhance language comprehension, but it does not confirm whether this system is necessary or sufficient to support such processing (Fischer and Zwaan 2008). In other words, neuroimaging techniques (e.g., fMRI, PET) studies can only tell us which brain regions participate in carrying out a given task. Even more, specific simulation properties of MNS may not be a causal mechanism, but a by-product of associative learning (Heyes 2010). In the same way, recent studies (Hickok et al. 2011; Rogalsky et al. 2011) have shown that selective damage in IFG (including Broca's area) does not predictably cause deficits in speech perception ability. The authors suggest that speculative strict version of MNS of language production/comprehension is untenable given the weight of the empirical evidence. In brief, MNS does not provide by itself a necessary and sufficient putative mechanism of action language understanding.

The somatotopy of the primary motor cortex and action-verb processing

Another body of evidence highlights the role of motor cortical areas in language processing. For instance, processing sentences or verbs describing actions performed by the mouth, hand or leg body segments has been shown to involve, the M1 and PMC, which are organized

somatotopically (that is, adjacent body muscles are represented in neighboring areas within the motor cortex). Although there is agreement that motor cortical areas are activated during action-verb processing, the exact characteristics of such activation are still under discussion.

One postulate is that overlap between motor activation and language processing can be understood on the basis of Hebbian associative learning principles (Hebb 1949). In this context, the strengthening of synaptic links must have a consequence of frequent coactivation of words describing actions and motor executions with nearly simultaneous presentation. This would trigger word-related overlapping networks of M1 and PMC in a somatotopic fashion (Hauk et al. 2004; Pulvermüller 1996; Pulvermüller et al. 2005).

However, some criticisms have been raised about the radical hypothesis of motor–language interaction (Mahon and Caramazza 2008; Toni et al. 2008; Louwerse and Juniaux 2008; Willems and Hagoort 2007). Kemmerer and Gonzalez-Castillo (2010) have shown that the somatotopic coordinates reported in previous studies do not overlap with probabilistically defined maps of the M1 and PMC. Moreover, the spatial coordinates reported show great variability (Aziz-Zadeh et al. 2006). In addition, some studies have failed to support somatotopic findings (Arevalo et al. 2012; Postle et al. 2008; Tremblay and Small 2011). Moreover, Tomasino et al. (2008) have shown that activation in M1 is enhanced for explicit motor imagery performed on action-verbs than for action-word comprehension per se. Furthermore, lesions of the motor cortex do not predictably cause deficits in action-word processing (Saygin et al. 2004). Finally, PMC cortex impairments produce action-verb processing alterations (e.g., Bak et al. 2001, 2006; Tranel et al. 2001, 2003). The strictly organized homunculus seen within the sensory and motor cortices is not evident within the PMC. Although some regions of the PMC can be broken down into multiple subdivisions (Aziz-Zadeh 2012), the specific role of PMC that responds to linguistic stimuli remains an open question. Moreover, the PMC seems to form a core part of neural network involved in abstract cognitive processes (Schubotz and von Cramon 2001; Schubotz et al. 2003). Once again, a simple causal mechanism of cortical motor system as putative origin of action language seems to be at least problematic.

New approaches of action/verb processing

The embodied framework has triggered intense discussions (Hickok 2009; Mahon and Caramazza 2008; Negri et al. 2007; Toni et al. 2008; Willems and Hagoort 2007). The critical evidence reviewed above suggest that MNS and cortical motor somatotopy are not sufficient in explaining how our brain processes action meaning and the engagement of other cortical regions is clearly required (Brass

et al. 2007). Moreover, converging evidence from PD and other findings suggest a more complex relationship between language and the motor system by showing a bidirectional influence of motor and language areas, including subcortical motor areas and even non-motor regions.

Accordingly, more lenient versions predicting partially overlapping (but not identical) regions comprising a general motor–language network have been proposed. These interpretations come from studies reporting activity in regions outside the M1/PMC such as the IFG, the temporal cortex, the cerebellum and the inferior/superior parietal lobule (de Zubicaray et al. 2010; Gazzola and Keysers, 2009; Kemmerer and Gonzalez-Castillo 2010; Pobric and Hamilton 2006).

Within the network approach the BG would play a crucial role in language functions. This role would open a new path for research in both normal and affected motor–language interaction. Considering that the origin of PD is mainly associated with subcortical structures, their action-verb processing impairments are probably not restricted to cortical areas (motor and language systems). In fact, this review provides evidence that action-verb processing also depends on a non-somatotopic BG involvement. Along these same lines, the BG have numerous connections with cortical areas that are active during language and semantic tasks. The role of action experiences during language understanding, claimed by several embodied cognition theories, can be supported by the BG. For instance, the motor and non motor learning of habits, a well-known function of the BG (Ashby et al. 2010; Graybiel 2008), may represent a decisive learning mechanism involved in the semantic grounding of action language.

Thus, a coupling model of motor and language systems would be a better explanation than a causal motor model of language. A less controversial claim may be supported by the partial overlap of language and motor cortical networks. This hypothesis suggests that action-verb processing depends on motor cortex integrity but does not claim a strict somatotopic relation or a causal involvement of the motor cortex, or a single MNS explanation. A bidirectional coupling between motor areas (cortical and subcortical) and language areas (e.g., STS, anterior and medial temporal pole) may provide a more parsimonious explanation of the interaction between motor and language networks.

Opening a new branch of research

Defining the functional organization of motor–language networks will lead to important insights regarding the role of the BG in the motor grounding of language. Future studies are needed to determine the specific cortical-subcortical networks that underlie the role of the BG in action-

verb processing. In addition, further neuroimaging and neurophysiological studies in patients with motor system diseases could shed light on the intricate effective connectivity patterns between language and motor areas.

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