The dissociability of lexical retrieval and morphosyntactic processes for nouns and verbs:

A functional and anatomoclinical study

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ABSTRACT

Nouns and verbs can dissociate following brain damage, at both lexical retrieval and morphosyntactic processing levels. In order to document the range and the neural underpinnings of behavioral dissociations, twelve aphasics with disproportionate difficulty naming objects or actions were asked to apply phonologically identical morphosyntactic transformations to nouns and verbs.

Two subjects with poor object naming and 2/10 with poor action naming made no morphosyntactic errors at all. Six of 10 subjects with poor action naming showed disproportionate or no morphosyntactic difficulties for verbs. Morphological errors on nouns and verbs correlated at the group level, but in individual cases a selective impairment of verb morphology was observed.

Poor object and action naming with spared morphosyntax were associated with non-overlapping lesions (inferior occipitotemporal and fronto-temporal, respectively). Poor verb morphosyntax was observed with frontal-temporal lesions affecting white matter tracts deep to the insula, possibly disrupting the interaction of nodes in a fronto-temporal network.

Keywords: Noun/Verb dissociations; Noun/Verb retrieval impairment; Nominal/Verbal morphosyntactic impairment; Fronto-temporal verb network

1. INTRODUCTION

Dissociations between nouns and verbs have been repeatedly documented in the neuropsychological literature (for reviews, see Shapiro & Caramazza, 2003a; Pillon & d'Honincthun, 2011; Vigliocco, Vinson, Druks, Barber, & Cappa, 2011). However, the reasons for such dissociations, and their implications for the neurofunctional architecture of language processes are still a matter of debate. This is because the processes underlying the production of nouns and verbs even in minimal syntactic context are complex. Nouns and verbs are content words, and as such are retrieved in the lexicon from semantic information about objects and actions, respectively. However, producing a verb or a noun in a sentence context also requires morphosyntactic operations, as roots must be combined with inflectional morphemes. As a consequence of such intricacies, the mechanisms underlying the separability of nouns and verbs at various processing levels are not yet clear. We set out to document the neural and functional underpinnings of action and object naming, and of nominal and verbal morphosyntactic processes, based on the performance of aphasic individuals.

1.a. Behavioral dissociations of noun/verb processing

According to some authors, dissociations are rooted in semantics, and result from damage to distinct meaning features of objects and actions (e.g. Damasio & Tranel, 1993; Daniele, Silveri, Giustolisi, & Gainotti, 1993; Daniele et al., 1994; Bird, Franklin, & Howard, 2000; Pulvermüller, Lutzenberger, & Preissl, 1999; see also Vigliocco et al., 2011; Kiefer & Pulvermüller, 2012, for reviews). Objects, which mainly correspond to nouns, are more concrete, referential and imageable; whereas actions, which mostly correspond to verbs, are more abstract, less referential, and characterized mainly by movement/motor attributes. Damage to a modality-specific semantic subsystem or to a specific set of semantic features will

disproportionately impair concept categories whose exemplars critically depend on them. For example, selective deficits for nouns could result from damage to regions associated with the processing of semantic features of objects (middle and inferior temporal lobe), whereas damage to areas involved in movement and motion coding (prefrontal regions) would more selectively affect verbs (Gainotti, Silveri, Daniele, & Giustolisi, 1995). On a different, but still semantically-based account (Vigliocco et al., 2011), dissociations would stem from the "event" vs "object" nature of a word, and therefore cross grammatical class boundaries, for example affecting nouns and verbs with similar meanings (e.g., in Italian, *camminata*, the walk, and *camminare*, to walk; *lettura*, the reading, and *leggere*, to read).

Although semantically-based accounts can accommodate some reports of noun/verb dissociation, in other cases the disorder cannot be easily ascribed to semantic damage. For example, modality-specific (written or oral) noun/verb dissociations strongly point to a lexical (grammatical class) impairment (Caramazza & Hillis, 1991; Hillis & Caramazza, 1995; Hillis, Tuffiash, & Caramazza, 2002; Hillis, Wityk, Barker, & Caramazza, 2002; Rapp & Caramazza, 2002), as only an intact semantic representation can support normal performance in the preserved modality.

Noun/verb dissociations may also be determined by grammatical-level impairments, as shown by disproportionate damage to nominal or verbal morphosyntactic processes (Shapiro, Shelton, & Caramazza, 2000; Thompson, Fix, & Gitelman, 2002; Tsapkini, Jarema, & Kehayia, 2002; Shapiro & Caramazza, 2003a, b; Laiacona & Caramazza, 2004). Subject JR (Shapiro et al., 2000), who named nouns significantly less accurately than verbs, showed an analogous dissociation when asked to complete sentences with homonyms by adding or removing a phonologically identical nominal or verbal suffix. He produced singular and plural noun forms (*This is a sail* ↔ *These are sails*) less accurately than he produced the same words as the 3rd singular or 3rd plural form of a verb (*This man sails* ↔ *These people sail*). The reverse dissociation was observed in RC (Shapiro & Caramazza, 2003b) and MR (Laiacona & Caramazza, 2004), who named actions less accurately than objects, and made more inflectional errors on verbs than on nouns. JR

and RC showed an analogous performance profile when performing morphological operations on pseudonouns and pseudoverbs (*This is a wug* ↔ *These are wugs*; *This man wugs* ↔ *These people wug*). These last results suggest selective damage to grammatical-class-specific computational processes, rather than to stored lexical-semantic features of words, since pseudowords do not have meaning, nor are they represented in the lexicon.

A different performance profile was documented in EA (Laiacona & Caramazza, 2004) and HG (Shapiro & Caramazza, 2003c). They presented with disproportionately poor retrieval of nouns (EA) and verbs (HG), respectively, but performed accurately in morphosyntactic tasks. Since items were matched for imageability and concreteness, these results are unlikely to stem from a semantic deficit. Dissociated performance on picture naming and morphosyntactic tasks suggests that the retrieval of a word belonging to a given grammatical category and the morphosyntactic operations associated with that category are mediated by at least partially separable neurofunctional substrates.

Results obtained by EA and HG are not entirely unproblematic, however. Poor naming of items belonging to a grammatical category in the face of errorless performance on morphosyntactic tasks involving the same category may result not so much from genuine sparing of morphological operations, but from the fact that those operations are easy enough as to be performed accurately even in the face of impaired inflectional processing. Indeed, both the nominal paradigm in Italian (intact in EA) and the verbal paradigm in English (intact in HG) are so skeletal that, in principle, they could be handled successfully even in the presence of brain damage. Furthermore, in languages with very simple morphology, errors in morphological transformation tasks may be difficult to adjudicate. For example, in English a "morphological" error like *"They sail; he …"* → *"sail"* might have a morphological cause (i.e., failure to manipulate the verb inflection), but also a non-morphological origin (e.g., it could be a perseveration).

Such an alternative account would be harder to maintain in a language in which the impaired category has a rich morphological paradigm. This would be the case of verbs in Italian. Regular Italian verbs belong to three different conjugation classes, and take 46 different forms depending on tense, person, aspect and number features. This contrasts with regular English verbs, which only have four synthetic forms (e.g. *play*, *plays*, *played*, *playing*), and derive other forms via analytic processes by combining an auxiliary with the base form (e.g. *will play*, *would play*). The complexity of the Italian verb paradigm rules out successful processing of verbal inflections in the presence of morphosyntactic impairments. Therefore, dissociations between verb retrieval and morphosyntax in Italian would strongly support the notion that the two sets of processes are functionally and neurally distinguishable. In order to document the range of disorders in Italian participants with aphasia, tasks requiring naming and morphosyntactic transformations of nouns and verbs were administered, focusing on the dissociability of lexical retrieval and morphosyntactic processes.

1.b. The neural underpinnings of lexical retrieval and morphosyntactic processes of nouns and verbs

Most studies investigating the functional neuroanatomy of the noun/verb distinction focused on lexical retrieval, as measured by action and object naming performance (e.g. Goodglass et al., 1966; Miceli et al., 1984; McCarthy & Warrington, 1985; Miceli et al., 1988; Damasio & Tranel, 1993; Daniele et al., 1993, 1994; Robinson et al., 1999). These studies typically associate noun retrieval deficits with left temporal lesions, and verb retrieval impairments with left prefrontal damage (e.g. Damasio & Tranel, 1993; Daniele et al., 1994; Shapiro & Caramazza, 2003b; see also Aggujaro, Crepaldi, Pistarini, Taricco, & Luzzatti, 2006; Crepaldi, Berlingeri, Paulesu, & Luzzatti, 2011). The inferior and middle frontal gyrus were found to be critical for verb processing also in individuals undergoing cortical mapping during awake surgery for the removal of gliomas (Havas et al., 2015).

More heterogeneous results have been reported in neuroimaging investigations. Many studies converge with lesion data. Left inferior prefrontal activity was observed in action naming (Perani et al., 1999; Tranel, Martin, Damasio, Grabowski, & Hichwa, 2005), in processing tense markings for regular and irregular verbs (Dhond, Marinkovic, Dale, Witzel, & Halgren, 2003; Oh, Tan, Ng, Berne, & Graham, 2011; Tyler, Stamatakis, Post, Randall, & Marslen-Wilson, 2005; Beretta et al., 2003; de Diego-Balaguer et al., 2006; Sahin, Pinker, & Halgren, 2006), and in the assignment of argument structure (Shetreet, Parti, Friedman, & Hadar, 2007). Increased prefrontal activity during verb (in comparison to noun) inflection processing has been attributed to the greater complexity of verbal morphosyntax in the languages under exam (Vigliocco et al., 2011). On the whole, however, and in partial contrast to lesion data, neuroimaging investigations tie verb processing to a more distributed neural network, whose nodes contribute differently to the processing of specific features. Thus, lateral temporal cortices have been involved in verb naming (Perani et al., 1999; Tranel et al., 2005), in processing verb-specific syntactic information (Bedny & Caramazza, 2011) and aspect markers (Yu, Bi, Han, & Law, 2013), and in retrieving argument structure (Shetreet et al., 2007). In addition, posterior parietal regions have been linked to thematic role assignment (Kielar, Milman, Bonakdarpour, & Thompson, 2011; Thothathiri, Kimberg, & Schwartz, 2012; Finocchiaro, Capasso, Cattaneo, Zuanazzi, & Miceli, 2015).

A lesion study focusing on 6 verb processing tasks (picture naming, picture comprehension, verb attribute, verb comparison, picture attribute, picture comparison) in 226 aphasic participants reconciles lesion and neuroimaging data. Lesions in the left inferior frontal gyrus were associated with poor performance on all six tasks, and perisylvian damage posterior to this region yielded poor scores on at least 4 (Kemmerer, Rudrauf, Manzel, & Tranel, 2012). In addition, verb processing was damaged in isolation by lateral temporal and parietal damage. These data do not challenge the view that verb processing mostly involves left prefrontal structures, nor that it does so more than nouns, but stress that multiple areas are involved in verb processing – including areas commonly thought of as being more critical for noun processing (see De Renzi & Di Pellegrino, 1995).

In contrast with the wealth of lesion data on the neural underpinnings of the noun-verb distinction at the word retrieval level, only seven neuroanatomical reports of dissociated morphosyntactic disorders for nouns and verbs are available (Shapiro et al., 2000 for JR; Thompson et al., 2002 for RB; Tsapkini et al., 2002 for SK; Shapiro & Caramazza, 2003c for RC and JR; Laiacona & Caramazza, 2004 for EA and MR). Lesions in these cases are extensive and heterogeneous. Therefore, while results support the separability of the neurofunctional representation of noun and verb morphology, they do not allow clear conclusions on the neural substrate of morphosyntactic operations. Some neurophysiological and neuroimaging investigations favor the hypothesis that specific prefrontal regions are critical for verb morphosyntactic processes. In rTMS studies, stimulation of the middle frontal gyrus anterior and superior to Broca's area selectively disrupted verb morphosyntax (Shapiro, Pascual-Leone, Mottaghy, Gangitano, & Caramazza, 2001; Cappelletti, Fregni, Shapiro, Pascual-Leone, & Caramazza, 2008). The same area was activated in an fMRI investigation (Finocchiaro, Basso, Giovenzana, & Caramazza, 2010). However, contrasting evidence was reported in other neuroimaging studies (e.g. Perani et al., 1999; Tyler, Bright, Fletcher, & Stamatakis, 2004; Sahin et al., 2006; Longe, Randall, Stamatakis, & Tyler, 2007; Bedny, Caramazza, Grossman, Pascual-Leone, & Saxe, 2008), and no systematic activations can be unambiguously linked to the manipulation of grammatical aspects of nouns and verbs. More recently, the hypothesis that greater left inferior prefrontal activity signifies specific involvement in morphosyntactic verb processing has been challenged, to favor the view that it aspecifically results from the greater complexity of verb morphology in the languages under study (Vigliocco et al., 2011). This view receives some support from an fMRI study in Chinese, a language with more complex noun than verb morphosyntax, showing increased left inferior frontal activity in response to nouns as compared to verbs (Yu et al., 2013).

In order to distinguish the neural underpinnings of action and object naming from those of nominal and verbal morphosyntactic processes, we analysed lesion data in twelve aphasic speakers with disproportionate impairment of noun or verb naming.

2. METHODS

2.1. Participants

Twelve native Italian speakers (6 males; age 23-78), who presented aphasia following a left hemisphere stroke, participated in this study. They were all right handers with at least 8 years of formal education (a 5th grader was also included, as his actual educational level was higher), had no history of alcohol abuse, and did not use psychotropic drugs. Neuroradiological documentation (CT or MRI) was available in all cases. Essential epidemiological information is reported in Table 1. Brain regions damaged in each subject are reported in Table 2. Participants provided informed written consent. The study was approved by the Ethical committee of the University of Trento.

[Tables 1 and 2 about here]

2.2. Experimental tasks

Participants were recruited because they presented with dissociated performance in the action vs object naming tests of a standard battery for aphasia (B.A.D.A., Miceli, Laudanna, & Capasso, 2006). To establish if subjects with disproportionate difficulty naming verbs or nouns also had a similar difficulty with morphosyntactic processes, tasks requiring the ability to manipulate noun and verb inflections were administered.

2.2.1. Object naming and action naming

The ability to retrieve nouns and verbs as lexical items was evaluated by administering the picture naming tasks of the B.A.D.A. Participants named 102 black-and-white drawings (oral naming: 30 nouns, 28 verbs; written naming: 22 nouns, 22 verbs). Items were balanced across lists for frequency of usage, length, age of acquisition, familiarity, and picture complexity. Only responses unambiguously attesting to a difficulty in lexical retrieval were scored as errors. Therefore, semantic substitutions, circumlocutions and failures to respond were scored as incorrect responses, whereas phonetic/phonemic and orthographic errors were scored as correct responses.

2.2.2. Morphological transformation (words)

Italian has six nominal paradigms, two of which are gender-transparent (1st class: masculine, singular ending -o, plural ending -i, e.g. il gatto [the cat] → i gatti [the cats]; 2nd class: feminine, singular ending -a, plural ending -e, e.g. la palla [the ball] → le palle [the balls]). In the present task, only gender-transparent nouns were used (masculine nouns as targets; masculine and feminine nouns as fillers). As to the verbal paradigm, there are three conjugations (first: parl-are [to speak], second: ved-ere [to see], third: dorm-ire [to sleep]). All the verbs have the same endings in the 1st (-o) and 2nd (-i) singular of the present indicative, irrespective of conjugation (e.g. io parlo [I speak], io vedo [I see], io dormo [I sleep]; tu parli [you speak], tu vedi [you see], tu dormi [you sleep]), but differ in other forms. For example, the 3rd singular of the present indicative ends in -a in first conjugation verbs (e.g. lui parla [he speaks]), but in -e in second and third conjugation verbs (e.g. lui vede [he sees], lui dorme [he sleeps]). In the present task, only the first three persons of the present indicative were used (1st and 2nd singular forms as targets, 1st, 2nd and 3rd singular forms as fillers).

Participants were asked to apply morphological transformations to 120 noun/verb homonyms (2 subjects completed a longer version of the task, and one a shorter version). Noun stimuli required transforming a masculine singular noun into a plural form or the reverse transformation (*il bacio* [the kiss, m.s.] ↔ *i baci* [the kisses, m.pl.]; *il ricamo* [the embroidery, m.s.] ↔ *i ricami* [the embroideries, m.pl.]). Verb items required transforming the 1st singular into the 2nd singular, or the reverse transformation (*io bacio* [I kiss] ↔ *tu baci* [you kiss]; *io ricamo* [I embroider] ↔ *tu ricami* [you embroider]). Target nouns were prompted by a definite article (*il tavolo* [the table, m.s.] → *i*…; *i tavoli* [the tables, m.pl.]→ *il*…) and target verbs by a personal pronoun (*io parlo* [I speak]→ *tu*…; *tu parli* [you speak]→ *io*…). The same phonological alternation was required in both cases (*o* ↔ *i*), but in the context of different morphosyntactic operations.

To discourage repetitive strategies, 120 fillers were also presented – 60 non-homophonic nouns (*la casa* [the house, f.s.] ↔ *le case* [the the houses, f.pl.]) and 60 non-homophonic verbs (*io rubo* [I steal] ↔ *lui ruba* [he steals]). Filler noun stimuli included feminine nouns. Filler verb stimuli required transforming the 1st or 2nd singular into the 3rd singular, present indicative, or viceversa. Nouns and verbs were balanced for syllabic complexity, length, and frequency of usage. Stimuli were administered orally in randomized sequence, in at least two separate sessions. The task was administered also to 20 matched control subjects, who performed flawlessly.

2.2.3. Morphological transformation (pseudowords)

To measure morphosyntactic abilities in the absence of semantic cues, a task requiring the transformation of 80 homonyms (40 pseudonouns and 40 pseudoverbs) was also prepared.

By analogy with the previous task, pseudonoun items required transforming a masculine singular stimulus into a plural form, or the reverse transformation (*il purfo* ↔ *i purfi*; *il nollempo* ↔ *i nollempi*), and pseudoverb items required transforming the 1st singular into the 2nd singular, or the reverse transformation (*io purfo* ↔ *tu purfi*; *io nollempo* ↔ *tu nollempi*). Even though the same phonological alternation (*o* ↔ *i*) was requested, the task required distinct morphological operations.

The test also included 20 non-homophonic pseudonoun and pseudoverb fillers (e.g., *la miva* ↔ *le mive*, *io ciso* ↔ *lui cisa*). Filler items included feminine pseudonoun and pseudoverb transformations involving the 3rd singular, present indicative. Pseudonouns and pseudoverbs were balanced for syllabic complexity, length, and Ncount (defined as the number of words obtained by changing one letter of the pseudoword at a time). This task was administered to 20 healthy controls. On the pseudonoun task, 1 subject produced 2 errors, 5 produced 1 error, and 16 performed flawlessly; on the pseudoverb task, 2 subjects produced 1 error, and 18 performed flawlessly.

This task was completed by 9 out of 12 aphasic participants. Subjects BRO and GMA found it exceedingly difficult, to the point that administration was discontinued. The task was not administered to FTE: in this subject, attempts to repeat isolated pseudowords yielded failures to respond, segmental and unrelated errors, and most incorrect responses were uninterpretable. Many participants experienced severe difficulties in repeating isolated pseudowords during the screening procedure, probably due to impaired phonological memory (for evidence from aphasia, see e.g., Martin & Saffran, 1990; Martin, Saffran & Dell, 1996). Since the mechanisms yielding pseudoword repetition difficulties could interefere in incontrollable ways also with performance on the morphosyntactic pseudoword task, the results of this latter task are interpreted very conservatively.

2.2.4. Data analysis

Errors in the morphosyntactic tasks were conflated into 2 macrocategories:

- morphological errors and errors with a morphological component: agreement, tense, gender, ending, nominalization, verbalization (these errors were counted as morphological also when they co-occurred with a non-morphological error on the stem);

- non-morphological errors: phonological errors, perseverations (on previous stimulus, or repetition of the current stimulus), semantic errors, neologisms, omissions.

Examples of morphological errors:

- agreement (e.g. stimulus: io rifiuto [I refuse, 1st sg. present], target: tu rifiuti [you refuse, 2nd sg. present], response: rifiuta [(he/she) refuses, 3rd sg. present]). Some incorrect responses classified as agreement errors resulted in stimulus repetition (e.g. stimulus: il grillo [the cricket, m. sg.], target: i grilli [the crickets, m. pl.], response: grillo [cricket, m. sg.]). These errors are discussed in the Results section;
- tense (e.g. stimulus: io volo [I fly, 1st sg. present], target: tu voli [you fly, 2nd sg. present], response: volerai [you will fly, 2nd sg. future]);
- gender (e.g. stimulus: le capanne [the huts, f. pl.], target: la capanna [the hut, f. sg.], response: capanno [the hut, m. sg.]);
- ending (e.g. stimulus: io freno [I brake, 1st sg. present], target: tu freni [you brake, 2nd sg. present], response: *frene);
- nominalization (e.g. stimulus: tu salti [you jump, 2nd sg. present], target: io salto [I jump, 1st sg. present], response: un salto [a jump, m. sg.]);
- verbalization (e.g. stimulus: il soffio [the blow, m. sg.], target: i soffi [the blows, m. pl.], response: egli soffia [he blows, 3rd sg. present]).

Examples of non-morphological errors:

- phonological error (leading to a nonword, e.g. stimulus: la truffa [the fraud, f. sg.], target: le truffe [the frauds, f. pl.], response: *cruffe; leading to a real word, e.g. stimulus: le note [“he notes, f. pl.], target: la nota [the note, f. sg.], response: moda [fashion, f. sg.])
- perseveration (e.g. stimulus: tu calcoli [you calculate, 2nd sg. present], target: io calcolo [I calculate, 1st sg. present], response: tu calcoli [you calculate, repetition of the stimulus]; or io raccolgo [I pick, 1st sg. present of a previous stimulus]);
- semantic error (e.g. stimulus la gallina [the hen, f. sg.], target: le galline [the hens, f. pl.], response uova [eggs, f. pl.]);
- neologisms (e.g. stimulus: tu salti [you jump, 2nd sg. present], target: io salto [I jump, 1st sg. present]; response: *bolino);
- omission (no verbal output for >10 seconds following the stimulus).

2.3. Lesion data

MR or CT images were available. Neuroradiological exams were carried out at different clinical sites, outside of standardized protocols, using different scanners, and over a long period of time. In some cases images were available on film, but not in digital format. For all these reasons, only qualitative analyses were conducted.

Images were analysed by an expert who was blind to the language deficits of each participant (SM). Lesion localization was obtained using T1-weighted MRI images or CT images. Hypointense/Hypodense regions appearing to be abnormal as compared to homologous regions of the unaffected

hemisphere were considered to be damaged. Anatomical lesion boundaries were identified on the basis of a CT brain atlas (Damasio & Damasio, 1989) and of an MRI brain atlas (Damasio, 2005). Both atlases provide a collection of brain images obtained in a single brain by using axial cuts with different angles, in order to guarantee that a structure identified in a section taken at a given angle is also present in a section taken at another angle that intersects it.

To identify the lesion site in each subject the following procedure was followed: 1) the incidence closest to the MRI or CT plane of acquisition was identified for each patient, 2) the principal sulci (central sulcus, precentral and postcentral sulci, superior and inferior temporal, superior and inferior frontal, intra-parietal sulcus and occipito-parietal sulcus) were identified and used as landmarks on the patient images and atlas section, 3) damaged tissue was identified. Moreover, making reference to sulci and gyri, the lesioned area was manually traced with MRIcro (www.mricro.com) on a MNI (Montreal Neurological Institute) template. Lesions were subsequently overlapped, in order to obtain images corresponding to the distribution of brain damage within each patient group, and to describe differences across groups. The presumed extent of damage to subcortical fiber systems was inferred by matching lesion reconstructions with available DTI atlases (Oishi, Faria, van Zjil, & Mori, 2011; Catani & Thiebaut de Schotten, 2012).

3. RESULTS

[Table 3 about here]

3.1. Object vs action naming: Functional and neural dissociations

Evidence supports and replicates the functional and anatomical dissociability of action and object naming. Two subjects (RPE and GIZ) fared significantly worse on nouns than on verbs; the remaining ten participants showed the reverse pattern of performance.

Intrahemispheric lesion sites in the two groups do not overlap (see Figure 1). In patients with selective damage to object naming, lesions involve the left posterior cerebral artery and overlap in the fusifom and lingual gyri, extending to the white matter of the temporal lobe. By contrast, in subjects with disproportionate impairment of action naming, lesions typically involve the anterior branches of the left middle cerebral artery. They overlap in the inferior frontal gyrus, and extend to the insula and the anterior portion of the superior temporal gyrus. White matter is damaged in regions where DTI atlases locate the superior longitudinal, arcuate, uncinate and inferior fronto-occipital fasciculi. These observations confirm previous lesion data (e.g. Damasio & Tranel, 1993; Daniele et al., 1994; Shapiro & Caramazza, 2003b; see also Aggujaro et al., 2006; Crepaldi et al., 2011).

[*Figure 1* about here]

As a next step, individual performance on the morphosyntactic task was considered, in order to evaluate the functional and neural correlates of morphosyntactic processes.

3.2. The relationships between naming performance and morphological transformations

3.2.1. Subjects with disproportionate impairment of object naming

Neither GIZ nor RPE made inflectional errors on the morphosyntactic task. GIZ produced many non-morphological errors on verbs, all but one resulting in stimulus repetition. Based on his behavior in other language tasks, we interpret these errors as perseverations (e.g., in a 108-item object naming battery, 33% of overall responses and 65% of errors were perseverations).

The performance of these two subjects is similar to that of EA (Laiacona & Caramazza, 2004), who also suffered from left temporal damage. It shows that morphological operations on nouns may be spared in the face of lexical-semantic impairment, as indexed by poor object naming. Sparing of morphosyntax is further confirmed by performance on pseudowords. RPE's performance was errorless, and GIZ produced only 1 inflectional error on a pseudonoun.

3.2.2. Subjects with disproportionate impairment of action naming

Ten subjects named actions significantly worse than objects. As a first step, we evaluated whether performance accuracy in action naming and in the morphosyntactic task were correlated. Naming errors resulting from failure to retrieve the target verb (semantic paraphasias, circumlocutions, failures to respond) and errors on verb inflections in the morphosyntactic task were considered. In the morphosyntactic task, the number of trials was not the same for the 10 participants; therefore, morphological errors were considered as percentages and submitted to an angular transformation. The statistical analysis fell far short of significance (Pearson's $r = .228$, $df=8$, ns, and Student's $t < 1$, ns). This result supports the notion that verb retrieval and inflectional verb processes are functionally independent and imply at least partly distinct neural substrates.

Participants with disproportionately poor action naming showed a wide range of performance on the morphosyntactic task. Six subjects (CDS, FTE, GPO, GMA, BRO, and ROR) produced verb inflections significantly less accurately than noun inflections. In two cases (MBR and FVA) a nonsignificant trend in the same direction was observed. The remaining two subjects (MGA and RLO) did not produce inflectional errors on verbs, despite very poor action naming.

The relationship between verb and noun morphology

With the exception of GPO (and, to a lesser extent, GMA), errors on noun morphology are either absent or very rare in subjects with poor action naming – even in those who produce very many errors on verb inflections, like CDS and FTE. A reliable account of relative sparing of noun morphology is difficult, given the features of Italian noun morphology. Since most Italian nouns only have singular/plural alternations, an inflectional error will result in stimulus repetition. For example, given a noun in the singular, a morphological error due to an inability to produce the plural form will typically yield repetition of the stimulus (e.g., *il salto*, the jump, *i*… → *salto*, instead of the expected *salti*, jumps, and vice versa). However, the same errors could also result from a non-morphological impairment (attentional deficits, perseverative behaviour, working memory limitations, etc.). Very different considerations apply to verbs. Since verb morphology is substantially more complex than noun morphology, a genuinely morphologically-based error on a verb will typically yield an incorrectly inflected verb form, rather than a repetition of the stimulus. With verbs, stimulus repetition is likely to result from non-morphological damage.

Given the difficulty in interpreting noun responses resulting in stimulus repetition, these errors were analysed in two ways. They were scored as non-morphological on a first pass, and as morphological on a second pass. In both cases, a highly significant correlation between inflectional errors on verbs and nouns was observed (Pearson's *r*: 0.815; p = .004; and Pearson's *r*: 0.858; p = .001, respectively). Interestingly, when repetition errors were counted as inflectional (i.e., when errors scored as morphosyntactic were potentially inflated by including incorrect responses that may be due to non-morphological mechanisms), the chi-squared difference between morphosyntactic errors on verbs vs nouns remained significant ($p<.05$) in 5/6 cases (CDS, FTE, BRO, GPO, and GMA). It dropped below significance only in ROR, who on this count produced incorrectly 4/60 (6.7%) verb inflections and 1/60 (1.7%) noun inflections – a stimulus repetition ($\chi^2 = 1.88$, p = n.s.).

Overall, results confirm the dissociability of inflectional noun and verb processes. Six subjects fared significantly worse on verb than on noun inflections.

Performance in the morphosyntactic pseudoword task

Most aphasic participants repeated nonwords poorly during the screening procedure already. Since the deficits underlying poor nonword repetition may interact with disrupted morphosyntactic processes in incontrollable ways, performance on this task is considered only briefly.

Subjects CDS and GPO, who showed significantly greater difficulties on verb morphology in the real word task, obtained similar results in the pseudoword task. Subject ROR is less impaired, on both verbs and pseudoverbs, but the non-significant trend in the pseudoword task (p = .079) is in the same direction as the significant difference in the word task (p = .042). Subject MBR showed a similar pattern of performance. He made

insignificantly more inflectional errors on verbs (7/60, or 11.7%) than on nouns (2/60, or 3.3%) with real words ($\chi^2 = 3$; $p = .08$) and showed a similar, but statistically insignificant trend in the pseudoword task. Subject FVA failed to name 9/50 (18%) verbs, and presented with a mild but selective disorder for verb morphology in the morphosyntactic task (morphological errors on 3/60 verbs (5%) and 0/60 nouns). She performed normally in the pseudoword task (1 morphological error/40 pseudoverbs (2.5%), no errors on pseudonouns). Subjects MGA and RLO named actions very poorly (incorrect responses: 20/50, or 40%, and 28/50, or 56%, respectively), but made no morphological errors on verbs, and did not show disproportionate impairment of pseudoverb morphology. On these stimuli, RLO performed normally (1/40 inflectional errors, or 2.5%), and MGA was marginally impaired (3/80, or 3.8%). Subjects BRO, FTE and GMA did not complete this task.

Overall, results on this task confirm those on the morphosyntactic task using real words.

3.3. Neural correlates of morphosyntactic processes

The lesions observed in the10 participants with disproportionate impairment of action naming were considered, in an attempt at identifying the neural correlates of verb morphosyntax. Five subjects who made morphosyntactic errors on verbs (CDS, FTE, GMA, BRO and ROR), and two who did not make such errors (MGA and RLO) were retained for analysis. Subjects GPO and MBR were excluded from the first group due to the high number of errors on noun morphology (GPO) and comparable difficulties on noun and verb morphology (MBR), respectively. Subject FVA was excluded from the second group because, even though her difficulties were very mild, she did produce some inflectional errors on verbs. Results are shown in Figure 2.

[Figure 2 about here]

In the two subjects with poor verb naming and spared verb morphology, damage is heterogeneous. RLO's lesion involves the middle and inferior frontal gyrus, precentral and postcentral cortices and the anterior portion of the superior temporal gyrus, including the basal ganglia and extensively destroying white matter tracts in this region. MGA, who suffered from a severe arterial spasm of the left middle cerebral artery following surgery for a ruptured aneurysm, has two left-hemisphere lesions. The first involves the superior and middle temporal and angular gyri, while sparing inferior temporal regions. The second affects the periventricular white matter at the watershed between anterior and middle cerebral arteries, where it overlaps with RLO's lesion. Lesions in these two subjects overlap in a small subcortical region close to the lateral ventricle, roughly corresponding to the course of the corticospinal tract, of the cortico-ponto-cerebellar tract, possibly of part of the long segment of the arcuate fasciculus, and including the caudate body.

In the group with poor verb retrieval and poor verb morphology, the overlap is greatest (4/5 or 5/5 cases) in the inferior frontal gyrus, the insula, the planum polare, the superior temporal gyrus, the claustrum, the striate and the neighboring white matter structures, including the arcuate fasciculus, the posterior segment of the inferior longitudinal fasciculus, the inferior fronto-occipital fasciculus, and possibly the uncinate fasciculus. The frontal aslant tract, that might play a role in language functions (Catani et al., 2013) is affected in this group (but also in subjects with intact morphosyntactic processes). Comparison of the rightmost, sagittal sections in the two subgroups with poor verb naming (Figure 2) suggest that extensive damage to fronto-temporo-insular cortices and underlying white matter may yield morphosyntactic deficits. Partial sparing of these regions, while still sufficient to disrupt action naming, might prevent damage to verbal morphology. This possibility will have to be explored in future studies.

The involvement of the middle frontal gyrus in the patient group with morphosyntactic damage was evaluated in detail, given the critical role assigned to this region in studies with healthy subjects (Shapiro et al., 2001; Cappelletti et al, 2008; Finocchiaro et al., 2010). If the middle frontal gyrus is critical for the processing of verb morphology, it should be lesioned in subjects with damaged verb morphology and intact in subjects with spared verb morphology. With all the limitations inherent in lesion studies and small sample sizes, the observed neurofunctional correlation is less than stringent. The middle frontal gyrus is not directly affected in 4/5 (80%) subjects with morphosyntactic impairment, and is damaged in 1/2 (50%) subjects with spared morphosyntactic processes (RLO). In other words, 5/7 subjects (71.4%) do not show the expected lesion pattern. It is of course possible that subcortical damage disconnected the middle frontal gyrus from other regions critical for inflectional verb processes.

4. DISCUSSION

Many neuropsychological studies report on dissociations between nouns and verbs, but very few focus on the grammatical aspects of such dissociations. Prior to the present study, only 7 subjects were described with an emphasis on the ability to manipulate noun and verb morphology (Shapiro et al., 2000; Tsapkini et al., 2002; Thompson et al., 2002; Shapiro & Caramazza, 2003b; Laiacona & Caramazza, 2004). These studies suggest that nominal and verbal morphology can be selectively impaired following brain damage. However, with two exceptions (Tsapkini et al., 2002; Laiacona & Caramazza, 2004), they were conducted in English. Given that English morphology is very simple, it is not always clear whether poor performance was due to specific morphosyntactic impairments or reduced processing resources. Therefore, a first goal of this study was to document the spectrum of disorders of noun and verb processing in a morphologically richer language like Italian. We wished to confirm that the processes

underlying noun and verb retrieval can dissociate from each other and, more importantly, from those involved in morphosyntactic operations on the same items. Since detailed neuroanatomical data are available for only 4 subjects (Shapiro & Caramazza, 2003a, b; Laiacona & Caramazza, 2004), a further goal was to investigate the neural correlates of nominal and verbal morphosyntactic processes. Twelve Italian aphasics suffering from disproportionate retrieval difficulty for nouns or for verbs completed morphosyntactic tasks. Performance analysis allowed locating dissociations to the lexical-semantic level, to morphosyntactic processes, or to a co-occurrence of the two impairments.

Results confirmed the well-known dissociability between nouns and verbs at the lexical/semantic level. Two subjects fared worse on nouns, 10 fared worse on verbs. Both subjects with poor object naming (RPE and GIZ) processed nominal morphology flawlessly. The other ten participants, who named significantly fewer verbs than nouns, showed variable patterns of performance in the morphosyntactic tasks. Even though tasks required the same phonological alternations for nouns and verbs (*-o* ↔ *-i*), six subjects fared significantly worse on verb than noun morphology. In two cases (MGA and RLO), poor verb naming was associated with intact morphology. As for the remaining two subjects, inflectional processing was similarly impaired for nouns and verbs in MBR, and verb inflections were insignificantly worse in FVA.

Distinct lesion sites were documented in subjects with disproportionate damage to noun and verb retrieval. In the former, lesions overlapped in the inferomesial temporal lobe. In cases with poor verb retrieval a much larger area of lesion overlap was observed. Selective impairment of action naming was associated with superficial and deep damage to prefrontal regions (mostly affecting the inferior frontal gyrus but also the insula), and to the lateral aspect of the temporal lobe, involving the anterior and middle portions of the superior and middle temporal gyrus but sparing inferomedial structures. Prefrontal damage has been documented in previous studies (e.g. Miceli et al., 1984; McCarthy & Warrington, 1985; Miceli et al., 1988; Caramazza & Hillis, 1991; Damasio & Tranel, 1993; Daniele et al., 1994; Berndt et al., 1997a, b; Breedin et al., 1998; Robinson et al., 1999;

Kemmerer et al., 2012). Involvement of the lateral aspect of the temporal lobe is consistent with lesion data (Kemmerer et al., 2011), and with neuroimaging results (Perani et al., 1999; Tranel et al., 2005; Shetreet et al., 2007; Bedny & Caramazza, 2011; Yu et al., 2013). That more areas were affected in subjects with disproportionate difficulty naming actions than in patients with selective difficulty with objects probably reflects the fact that retrieving a verb in response to a picture requires more complex inferential processes than retrieving a noun. Verb production also requires the availability of more information, related to meaning (e.g., thematic role assignment), syntax (e.g., argument structure) and morphosyntax (more complex inflectional paradigm), than noun production. Retrieving such features might differentially engage distinct brain regions. Damage to each of these could cause, or contribute to, difficulty in action naming.

4.1. The relationships between lexical retrieval and morphosyntactic processes

The two subjects with disproportionately impaired object naming (GIZ and RPE) made no errors on nominal morphology, just like Italian-speaking subject EA (Laiacona & Caramazza, 2004). It is tempting to ascribe the lack of inflectional errors on nouns in these three subjects to the fact that skeletal noun morphology in Italian allows flawless production of noun inflections even in the face of mild nominal morphology impairment or reduced processing resources. Two facts from lesion studies argue against this possibility. First, morphosyntactic difficulties have been observed only in subjects with large left-hemisphere lesions, involving frontal as well as temporal and/or parietal regions. This is true not only for aphasic speakers with poor verb morphology (Shapiro et al., 2000; Tsapkini et al., 2002; Thompson et al., 2002; Shapiro & Caramazza, 2003b, c; Laiacona & Caramazza, 2004) but also for JR, the only subject reported thus far with selective damage to noun morphology (Shapiro et al., 2000). In our sample,

two subjects with poor verb retrieval and morphology (GPO and FTE) also made several errors on noun inflections. Both had extensive frontotemporoparietal damage. In other words, the lesions observed in subjects who make inflectional errors on nouns differ from those observed in the patients with poor noun retrieval but spared noun morphology (EA, Laiacona & Caramazza, 2004; GIZ and RPE), in whom lesions are restricted to the inferomesial portions of the temporal lobe. These observations encourage to argue that noun retrieval involves the temporal lobe (e.g., Shapiro, Moo, & Caramazza, 2006; Longe et al., 2007; Capitani et al., 2009; see Mätzig, Druks, Masterson, & Vigliocco, 2009 for review), and that processing noun inflections requires intact left prefrontal regions, which are part of a frontotemporal network involved in morphosyntactic operations (Miceli et al., 2002; Sahin et al., 2006; Carreiras et al., 2015). In this framework, errorless processing of noun inflections in EA, GIZ and RPE would result from true sparing of morphological processes, and not from Italian noun morphology being too easy to yield a noticeable error rate when damaged. By the same reasoning, inferotemporal activity in fMRI studies during the production of nominal inflections (Shapiro et al., 2005; Shapiro et al., 2006) is unlikely to reflect morphosyntactic processes.

Even though the performance of GIZ and RPE already supports the distinction between lexical/semantic and morphosyntactic processes, the strongest evidence for the neurofunctional separability of lexical retrieval and morphological operations is provided by MGA and RLO. They showed disproportionate difficulty naming actions, but intact verb inflections. A similar profile was reported in HG (Shapiro & Caramazza, 2003c), but the limited range of English verb morphology does not completely rule out that in his case verb inflections were produced accurately in the presence of mild morphosyntactic damage. This argument does not apply to Italian, whose verb morphology is much more complex. An analysis of the slips-of-the-tongue produced by speakers of Italian (Miranda, 1988) and English (Fromkin, 2007) informs on the relative difficulty of verb morphology in the two languages – Italian speakers are 4 times more likely to make morphological slips (3.2% vs 0.8% of the entire error corpus, respectively).

Therefore, an account of errorless performance on verb inflections based on simplified morphology is not tenable in Italian. The behavior of MGA and RLO provides strong evidence for the neurofunctional dissociability of verb retrieval and verb morphosyntax. This conclusion is further supported by the group analysis, that shows no correlation between accuracy in action naming and in morphosyntactic tasks.

Conclusive evidence for the separability of lexical retrieval from morphosyntactic processes would be provided by the complementary dissociation to that reported for MGA, RLO and HG – namely, good performance in verb naming and poor production of verbal inflections. Such cases were not expected in our sample, as participants were recruited based on disproportionate damage to noun or verb naming, not on difficulty in morphosyntactic tasks. Only subject CDS had more inflectional errors in the morphosyntactic task (41%) than retrieval failures in action naming – but, her naming error rate was also high (16%). However, the relevant dissociation has been reported. In spontaneous speech, cases described by Miceli, Mazzucchi, Menn & Goodglass (1983), Nespoulous et al. (1988), Caramazza and Hillis (1989), Thompson et al. (2002) did not omit main (lexical) verbs, but produced many incorrect inflections. Even if not specifically tested for noun/verb dissociations, these patients showed markedly impaired processing of free-standing and bound morphemes (i.e., omissions of function words and substitutions of infinitival for finite verb forms), but preserved lexical retrieval (i.e., no omissions of content words in obligatory contexts).

4.2. The neural substrate of morphosyntactic processing

While behavioural results clearly confirm the separability of inflectional processes and of lexical retrieval of action words, the attempt at differentiating their neural underpinnings was only partially successful (Figure 2). In participants with poor action naming and impaired verb

morphosyntax, left hemisphere damage involved superficial and deep prefrontal areas, including the insula, and extended to superficial and deep, anterior and superior areas in the lateral temporal lobe, disrupting fiber tracts between frontal and parietal regions. Notably, in four cases no direct damage was documented in the middle frontal gyrus, which has been considered crucial for verb inflection processing (Shapiro & Caramazza, 2003b, b; Cappelletti et al., 2008; Shapiro et al., 2006; Finocchiaro et al., 2010).

Two aspects of the lesions observed in the 10 subjects with disproportionately poor verb retrieval are worth considering. First, even though most of them (8/10) suffered from dorsolateral prefrontal damage, their lesions also involved, without exceptions, the anterior/superior temporal gyrus and the insula – this was true even for the two subjects (BRO and MGA) in whom no dorsolateral prefrontal damage was detected. Second, in all the subjects with morphosyntactic impairment and in neither of those with spared morphosyntax, damage to the superior lateral aspect of the temporal lobe extensively involved the underlying white matter (Figure 2(a) and (b), bottom rows).

With all the caution dictated by small sample size, data invite to consider the possibility that difficulty with verb inflections occurs when a superficial and deep lesion affects prefrontal regions extending to the insula, and the lateral aspect of the temporal lobe (superior and middle temporal gyrus). In this context, the meaning of insular involvement is unclear. While the role of the insula in the integration and awareness of cognitive, affective, somatosensory and autonomic information is supported by lesion and neuroimaging studies (for recent reviews, see Jones, Ward, & Critchley, 2010; Chang, Yarkoni, Khaw, & Sanfey, 2013), its role in language processes is underspecified. A meta-analysis of fMRI studies showed bilateral involvement of the insula in output and input language tasks, and involvement of the left insula in speech production tasks (Oh, Duerde, & Pang, 2014). A study of non-fluent variant PPA showed a correlation between atrophy of the superior precentral insular gyrus and speech production impairment (Mandelli et al, 2016). However, as in previous studies (Dronkers, 1996), the role putatively played by the insula is the coordination of

articulatory gestures during speech, and not morphosyntactic processing. This latter possibility was suggested by lesion reconstruction in 26 agrammatic speakers (Vanier & Caplan, 1990), where the insula was the area of greatest overlap. However, in middle cerebral artery strokes damage the insula also inevitably affects the underlying white matter, that includes components of the language network (e.g., uncinate fasciculus, inferior fronto-occipital fasciculus, inferior longitudinal fasciculus). Damage to these fiber tracts, rather than to the insula itself could be more directly responsible for poor performance on morphosyntactic tasks.

Difficulties with verb production might affect both lexical retrieval and morphosyntactic processes only when the lesion affects not only prefrontal and lateral temporal regions, necessary for verb naming, but also white matter connections between these regions and the prefrontal areas involved in inflectional processing. Data consistent with this possibility were reported in an fMRI study of agreement (Carreiras, Quiñones, Mancini, Hernández-Cabrera, & Barber, 2015). Involvement of a distributed neural network in verb processing is not surprising. Even in a simple subject-verb context, producing the correct finite verb requires the availability of lexical-grammatical (auxiliary, conjugation, transitivity, argument structure, etc.), semantic (tense, aspect) and morphosyntactic features (agreement), that can only result from concerted activity in a complex neural network.

4.3. The relationships between noun and verb morphology

Italian morphosyntax is substantially more complex for verbs than for nouns. Several participants showed significantly greater damage to verbal than nominal inflections, but the reverse pattern did not occur. In addition, damage to noun and verb inflections correlated, and none of the

participants showed severe damage to verb morphology in the face of complete sparing of noun morphology. With one exception (JR, Shapiro et al., 2000), also English-speaking aphasics showed disproportionate damage to verb morphosyntax.

These data, while consistent with the hypothesis that noun and verb morphology are functionally and (at least in part) neurally independent, encourage considering an alternative possibility. All morphosyntactic processes might share the same neural substrate, and clinical profiles that surface as *prima facie* dissociations might simply result from the relative complexity of verbal and nominal inflectional paradigms, rather than from a specific morphosyntactic impairment (Vigliocco et al., 2011). This possibility is supported by a recent fMRI study (Yu et al., 2013). Contrary to Italian and English, Chinese noun morphology includes many classifiers and is much more complex than verb morphology, which is limited to aspect features. In healthy Chinese participants, noun processing activated the left inferior frontal gyrus more than verb processing – i.e., the reverse picture to that documented for languages in which verb morphology is more complex than noun morphology. This result raises the possibility that the left prefrontal region is not specifically involved in morphosyntactic processing. Just as hypothesised in the case of semantic and phonological processing (Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Grindrod, Bilenko, Myers, & Blumstein, 2008; Righi, Blumstein, Mertus, & Worden, 2009), it might be active in morphological processing whenever selection is needed among items that compete at the same representational level. On this view, other brain areas would implement specifically morphological processes, some of which might involve prefrontal regions.

However intriguing, this possibility must be considered cautiously, for at least three reasons. English-speaking subject JR (Shapiro et al., 2000) fared worse on noun than verb morphology, even though the former is less complex than the latter. In Greek, both the nominal and the verbal inflectional system are rich, but subject SK (Tsapkini et al., 2002) was significantly more impaired on verb morphology (overall, he produced incorrectly 12/43 inflected verbs, or 27.9%; and 5/58 inflected nouns, or 8.6%). In our sample, five subjects were significantly more impaired on verb

than noun morphosyntax, even when stimulus repetitions counted as morphological (i.e., even when the occurrence of putative morphological errors on nouns was potentially inflated). And after all, in the light of the double dissociability of word retrieval and morphosyntactic processes, even if prefrontal structures only played an aspecific role in inflectional processes, one would still need to assume that some other brain regions are critical in that respect.

5. CONCLUSIONS

The processes involved in the retrieval of nouns and verbs are functionally separable, and are dissociable from those involved in morphosyntactic operations. The neural substrates that allow these distinctions are less clear. Lesion data suggest that noun and verb retrieval involve a mainly inferotemporal and a mainly prefrontal and lateral temporal substrate, respectively, and that morphological processes involve prefrontal regions. The co-occurrence of retrieval and morphosyntactic damage for verbs seems to require damage to a network that includes dorsolateral frontal and lateral temporal regions, and extensively disrupts white matter tracts deep to the insula.

Inflectional processing of nouns and of verbs in (even minimal) syntactic contexts may be achieved by different neurofunctional architectures. One possibility is that the same prefrontal substrate is shared by noun and verb morphology. On this view, the outcomes of morphosyntactic damage are determined by the complexity of morphology in the language – there should not be Italian aphasics with greater damage to noun than to verb morphosyntax, nor Chinese aphasics with the reverse profile. As an alternative, noun and verb morphology might be implemented in neighbouring but at least partially distinct neural structures, or in overlapping regions connected to other cortical structures by at least partially distinct fiber tracts. On

this view, morphosyntactic processes could be disproportionately impaired for nouns or for verbs, irrespective of language-specific morphological complexity.

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FIGURE LEGENDS

Figure 1. Lesion overlap in participants with significantly greater difficulty in (a) object naming (n=2) and (b) action naming (n=10).

Figure 2. Lesion overlap in participants with significantly greater difficulty in action naming who (a) achieved errorless performance in verb morphosyntactic tasks (n=2) and (b) fared poorly on morphosyntactic tasks, with significantly greater impairment on verbs than on nouns (n=5).

Table 1. Essential biographical and epidemiological information on participants.

	Gender	Age	Education	Time post-onset	Profession
GIZ	M	77	5	1y	Head of railway station
RPE	M	78	13	1y	Lawyer
CDS	F	44	8	4y	Homemaker
FTE	F	31	13	4y	Entrepreneur
GPO	M	50	15	4y	Entrepreneur
GMA	M	50	8	20y	Employee
BRO	M	61	18	3y	Entrepreneur
ROR	F	48	13	4y	Hotel owner and manager
MGA	F	44	13	3y	Homemaker
RLO	F	40	17	2y	Employee
FVA	F	45	18	2y	Musician
MBR	M	23	10	4m	Jockey

Table 2. Areas damaged by the lesion in each participant.

Patients	IFGpo	IFGpt	IFGporb	MFG	OFG	preCG	postCG	SMG	AG	preCun	STG	MTG	ITG	TOG	paHG	Hip	FusiG	LingG	Cun	Ins	Ca	Pu	Pa	Th
GIZ										+				+	+	+	+	+	+					
RPE												+	+	+	+									
CDS	+	+	+			+	+				+									+	+	+	+	+
FTE	+	+		+		+	+	+	+		+									+				
GPO	+	+		+		+	+	+			+	+								+	+	+	+	+
GMA	+	+				+	+				+									+	+	+	+	
BRO							+	+	+		+	+								+				
ROR	+	+	+			+	+	+			+	+								+		+		
MBR			+		+						+	+								+	+	+	+	
FVA	+	+				+	+				+					+				+	+	+		
MGA									+		+	+												
RLO	+	+		+		+	+				+					+				+	+	+	+	+

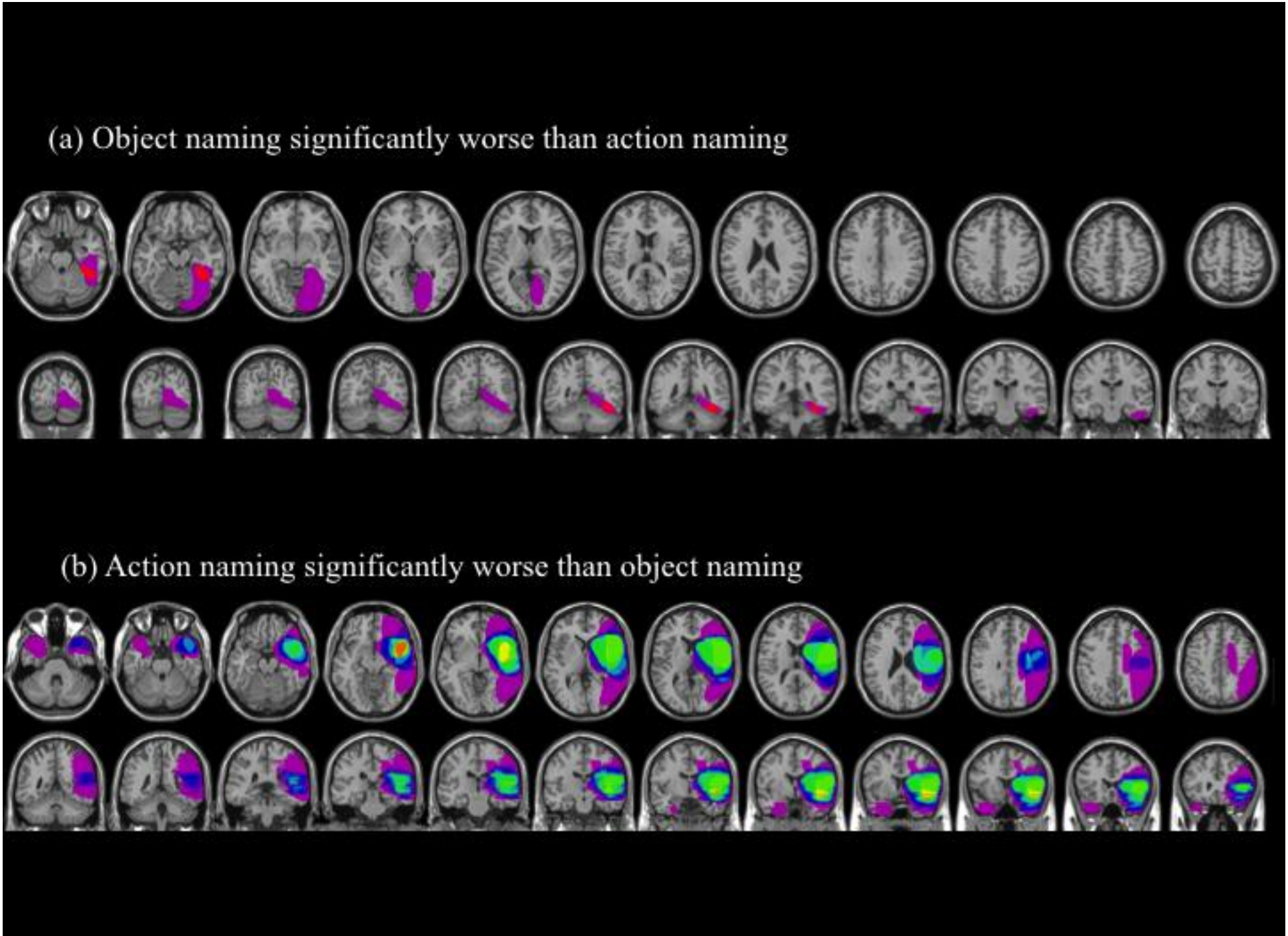
IFG=inferior Frontal Gyrus (po=pars opercularis; pt=pars triangularis; porb=pars orbitalis); MFG=Middle Frontal Gyrus; OFG=Orbital Frontal Gyrus; preCG= precentral Gyrus; postCG=postcentral Gyrus; SMG=Supramarginal Gyrus; AG=Angular Gyrus; preCun=precuneo; STG=Superior Temporal Gyrus; MTG=Middle Temporal Gyrus; ITG=Inferior Temporal Gyrus; TOG=Temporo-Occipital Gyrus; paHG=Paraippocapus Gyrus; Hip=Ippocampus; FusiG=Fusiform Gyrus; LingG=Lingual Gyrus; Cun=Cuneus; Ins=Insula; Ca=Caudate nucleus; Pu=Putamen; Pa=Pallidum; Th=Thalamus

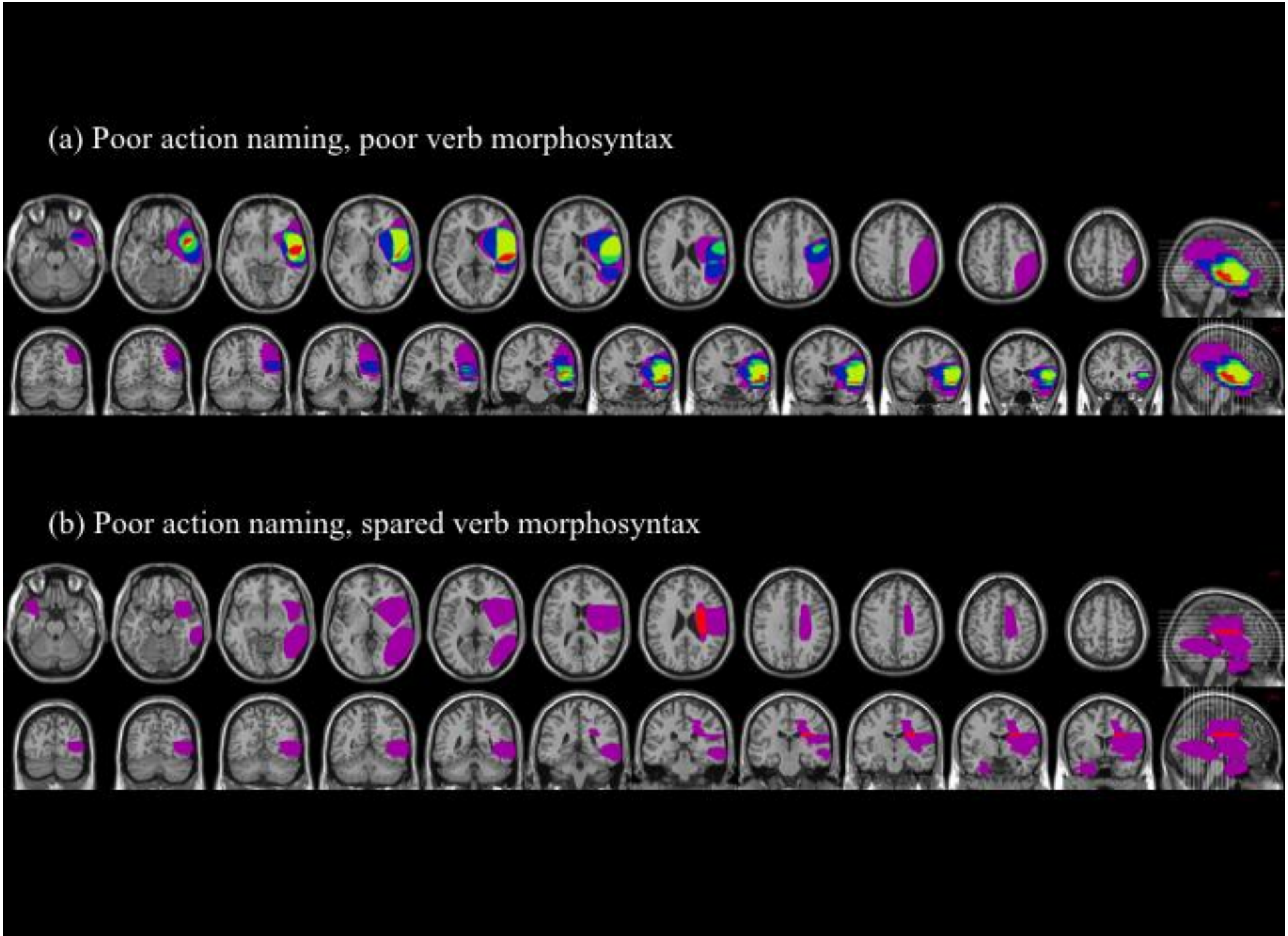
Table 3. Errors in the picture naming tasks (objects and actions) and in the morphosyntactic tasks. All chi-squares with df=1. Significantly different performances are in **bold**.

	Lexical errors in naming tasks			Morphological errors on morphosyntactic tasks			Morphological errors on morphosyntactic pseudoword tasks		
	Nouns (n=52)	Verbs (n=50)	chi-square values	nouns (n=60)	verbs (n=60)	chi-square values	pseudonouns (n=40)	pseudoverbs (n=40)	chi-square values
GIZ	**20.4%**	12.0%	χ^2=10.55 p <.001	0.0%	0.0%	χ^2=0 ns	0.0%	2.5%	χ^2=1.01 ns
RPE	**40.4%**	18.0%	χ^2=6.15 p=.013	0.0%	0.0%	χ^2=0 ns	0.0%	0.0%	χ^2=0 ns
CDS	3.8%	**16.0%**	χ^2=4.26 p=.039	1.1%	**23.3%**	χ^2=20.71 p<.001	12.5%	**35.0%**	χ^2=5.59 p=.018
FTE	11.5%	**40.0%**	χ^2=10.87 p<.001	1.4%	**28.9**%	χ^2=19.36 p<.001	not administered	not administered	
GPO	21.2%	**64.0%**	χ^2=19.19 p<.001	18.3%	**50.0%**	χ^2=13.37 p<.001	35.0% [(e)]	**60.0%** [(e)]	χ^2=7.52 p=.006
GMA	34.6%	**60.0%**	χ^2=6.59 p=.01	6.7%	**40.0%**	χ^2=9.32 p=.002	discontinued	discontinued	
BRO	3.8%	**18.0%**	χ^2=5.31 p=.021	0.0%	**6.7%**	χ^2=4.14 p=.042	discontinued	discontinued	
ROR	11.5%	**72.0%**	χ^2=19.24 p<.001	0.0%	**6.7%**	χ^2=4.14 p=.042	0.0%	5.0%	χ^2=3.08 ns
MBR	50.0%	**74.0%**	χ^2=6.22 p=.013	3.3%	11.7%	χ^2=3.0 ns	10.0%	17.4%	χ^2=0.95 ns
FVA	1.9%	**18.0%**	χ^2=7.45 p=.006	0.0%	5.0%	χ^2=3.08 ns	0.0%	2.5%	χ^2=1.01 ns

MGA	9.6%	**40.0%**	χ^2=12.72 p<.001	0.0%	0.0%	χ^2=0 ns	0.0%	3.8%	χ^2=3.06 ns
RLO	26.7%	**56.0%**	χ^2=5.55 p=.019	0.0%	0.0%	χ^2=0 ns	5.0%	2.5%	χ^2=0.35 ns

For each task, all subjects completed the number of items indicated in the Table, with the following exceptions.
Picture naming: RLO named 30 actions and 30 objects.
Morphosyntactic word task: two subjects completed shorter versions (RPE: 40 nouns and 40 verbs; GMA: 30 nouns and 30 verbs), two completed longer versions (CDS and FTE: 90 nouns and 90 verbs).
Morphosyntactic pesudoword task: three subjects completed longer versions (GPO and ROR: 60 pseudonouns and 60 pseudoverbs; MGA: 80 pseudonouns and 80 pseudoverbs).


(a) Object naming significantly worse than action naming
(b) Action naming significantly worse than object naming


(a) Poor action naming, poor verb morphosyntax
(b) Poor action naming, spared verb morphosyntax