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Review

Nouns and verbs in the brain: A review of behavioural, electrophysiological, neuropsychological and imaging studies

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ABSTRACT

In the past 30 years there has been a growing body of research using different methods (behavioural, electrophysiological, neuropsychological, TMS and imaging studies) asking whether processing words from different grammatical classes (especially nouns and verbs) engage different neural systems. To date, however, each line of investigation has provided conflicting results. Here we present a review of this literature, showing that once we take into account the confounding in most studies between semantic distinctions (objects vs. actions) and grammatical distinction (nouns vs. verbs), and the conflation between studies concerned with mechanisms of single word processing and those studies concerned with sentence integration, the emerging picture is relatively clear-cut: clear neural separability is observed between the processing of object words (nouns) and action words (typically verbs), grammatical class effects emerge or become stronger for tasks and languages imposing greater processing demands. These findings indicate that grammatical class per se is not an organisational principle of knowledge in the brain; rather, all the findings we review are compatible with two general principles described by typological linguistics as underlying grammatical class membership across languages: semantic/pragmatic, and distributional cues in language that distinguish nouns from verbs. These two general principles are incorporated within an emergentist view which takes these constraints into account.

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Grammatical class (nouns, verbs, adjectives, etc.) is one of the best candidates for being a linguistic universal. All languages have different parts of speech, and, most relevant here, all languages distinguish between nouns and verbs (albeit in different manners). This fact has been taken by some to indicate that grammatical class is one likely candidate for being part of a language organ, part of our genetic makeup and therefore behaviourally and neurally separable from other types of linguistic information (e.g., Pinker, 1994).

A radically different view of grammatical class is the one introduced by Sapir (1921) and more recently exemplified by functionalist approaches to language processing (e.g., Bates and MacWhinney, 1982), according to which grammatical class is a

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property emergent from semantic distinctions, and patterns of co-occurrences in language. Hence, grammatical class is neither behaviourally nor neurally separable from this other information (see also Elman, 2004). For example, Sapir (1921) wrote:

> "There must be something to talk about and something must be said about this subject of discourse [..] The subject of discourse is a noun. As the most common subject of discourse is either a person or a thing, the noun clusters about concrete concepts of that order. As the thing predicated of a subject is generally an activity [..], the form which has been set aside for the business of predicating, in other words, the verb, cluster about concepts of activity. No language wholly fails to distinguish noun and verb, though in particular cases the nature of the distinction may be an elusive one". (p.35).

The finding of a double dissociation, first reported in the late 1980s (e.g., Miceli et al., 1984, 1988; Zingeser and Berndt, 1988), between aphasic patients who were more severely impaired in producing nouns than verbs, and patients who showed the opposite pattern (greater impairment with verbs than nouns) has been taken as strong evidence in favour of grammatical class being an organisational principle of lexical knowledge in the brain (e.g., Caramazza and Hillis, 1991). This claim has been taken to imply that words that are nouns and words that are verbs in a language are represented in segregated (or at least partially segregated) neural networks in which left temporal areas would underscore the representation of nouns and left frontal areas the representation of verbs (e.g., Damasio and Tranel, 1993; Daniele et al., 1994).

While there are now more than 200 reported cases of patients showing noun-specific, or more often, verb-specific deficits (see Mätzig et al., 2009), the picture emerging from the neuropsychological literature is complex. In addition, functional imaging and electrophysiological studies have, for the most part, provided conflicting results concerning the anatomical substrate of grammatical class knowledge. In this paper we present a review of the extant literature, considering behavioural, electrophysiological, neuropsychological, TMS and imaging studies of the noun–verb distinction. Results obtained using these different methodologies are discussed in light of cognitive and neuroanatomical models of the representation and processing of grammatical class. As we will see, our conclusion is that the available evidence is compatible with views according to which words from different grammatical classes are processed by a shared network.

We focus on nouns and verbs, because these are the two classes that have been most extensively studied and for which the strongest claims of neural separation have been made. We will start by presenting a bird's eye view of cognitive and neuroanatomical hypotheses, and then review the existing literature considering behavioural, electrophysiological, neuropsychological, TMS and imaging studies.

1. Key issues and brief theoretical overview

Three key issues guide our review of the evidence. First is the extent to which studies distinguish manipulations of grammatical class and of semantics. Grammatical class is highly correlated with meaning: objects in the world are generally referred to using nouns, and actions are referred to using verbs. It is the case, however, that across languages the correlation between semantics and grammatical class is not perfect. Nouns can refer to events (*the walk*) and both nouns and verbs can refer to abstract concepts (e.g., *the love/to love*). The powerful correlation between semantics and grammatical class has both theoretical and methodological consequences. The former will be addressed in the general discussion, the latter, because any study in which grammatical class and semantic distinctions are confounded cannot be interpreted univocally. Therefore, studies must be designed in such a way as to tease apart semantics and grammatical class. By and large, this has not been the case in behavioural, neuropsychological and imaging studies. This is particularly true of the vast majority of lesion studies comparing aphasic and dementia patients' naming performance when presented with pictures of objects vs. when presented with pictures of actions.

The second key issue is methodological, and concerns whether the studies investigate processes of retrieval of lexical information from memory or, in addition, processes of lexical integration into sentences. Grammatical class is syntactic information about how to use words in sentences (and therefore is necessary for sentence integration), but is not essential lexical information, like a word's meaning or its phonological form (and therefore is not necessarily a part of the lexical information associated with a word that is retrieved from memory). Thus, intuitively, whereas grammatical class information is relevant to processing connected speech, it may not be relevant to the processing of words in citation form. As we shall see below, there is plenty of evidence that grammatical class information is relevant to understanding and producing sentences, but the situation is very different when considering single words.

The final key issue concerns differences in processing demands for nouns and verbs cross-linguistically. Across languages, it is generally the case that processing verbs in sentences is more demanding than processing nouns at a number of different levels. First, overall, verbs impose greater processing demands than nouns semantically: verbs refer to events, and events most often have multiple participants that need to be integrated; although nouns can also refer to events, typical nouns referring to objects, instead, refer to discrete entities. Second, verbs impose greater processing demands syntactically because their properties project onto other words (often nouns). For example, Baker (2003) argues that verbs must have a subject, and that only they can assign the thematic roles of agent and theme. Nouns are the receivers of thematic roles (they themselves cannot assign thematic roles). Only nouns (whether common or abstract) can act as the subject or direct or indirect object of a clause. Finally, verbs are more complex than nouns morphologically. Even in morphologically poor languages such as English, verbs have a greater number of morphologically inflected forms than nouns (four vs. two). Thus, in any task engaging integration processes, the processing demands for nouns and verbs may differ, with verbs necessarily involving greater processing demands. Cross-linguistically, these differences in processing demands can vary quite substantially. For example, languages greatly differ in the number of morphologically inflected forms for verbs and nouns. In English, a poorly inflected language, there are four possible verb forms and two noun forms. In a morphologically rich language such as Italian, there are more than 90 possible inflected verb forms (for each verb type) compared to only four possible inflected forms for nouns.

These three issues are often confounded in the literature, and are critical to our interpretation of reported findings both at the cognitive and neural level as we discuss below. Let us now provide a brief summary of psycholinguistic and neural models.

1.1. Psycholinguistic models

Fig. 1 sketches basic assumptions of relevant theories of language processing. We group theoretical proposals into three classes. In the first class of theories, grammatical class is specified at the lexical level. These are also known as *lexicalist* theories of sentence production and comprehension, based on the assumptions of *Lexical Functional Grammar* developed in linguistics (e.g. Kaplan and Bresnan, 1982; Bresnan, 2001). Lexicalist theories assume that grammatical class information is retrieved from memory during

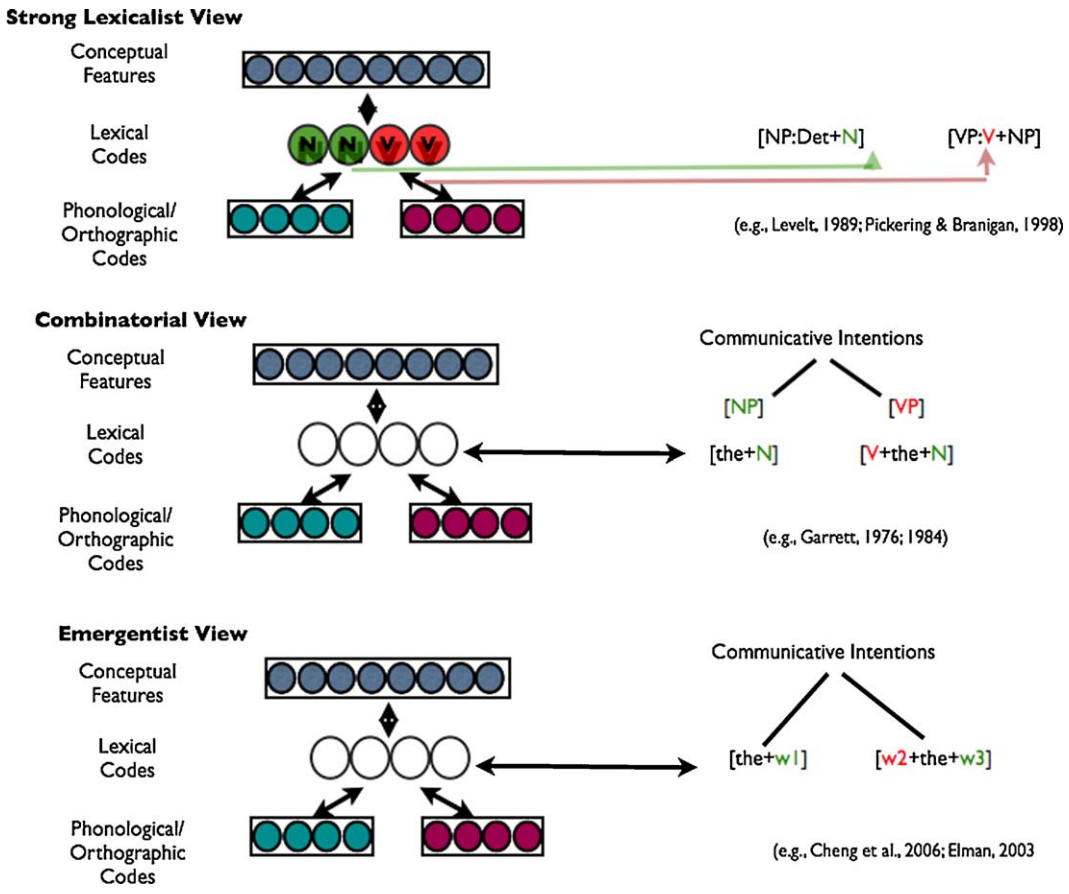

Fig. 1. Schematic overview of different theoretical positions concerning the processing of nouns and verbs. Theories are divided into broad classes differing on assumptions concerning the representation and recruitment of grammatical class information.

production or comprehension, like the meaning and phonology of a word. It is often assumed that lexically specified syntactic information (including grammatical class, but also other properties such as subcategorization frames and grammatical gender) guides the process of syntactic encoding in production and decoding in comprehension (see e.g., Levelt, 1989; Kempen and Hoenkamp, 1987). EEG studies indicate that in sentence comprehension, the grammatical class of a word is accessed very early (within the first 150 ms), which is compatible with its lexical status (e.g., Friederici et al., 2003). In word production, the finding that grammatical class is preserved in nearly *all* lexical errors (e.g., saying "dog" when "cat" is intended, Garrett, 1980) is also compatible with the lexical representation of grammatical class (Levelt, 1989). In a strong version of a lexicalist view, exemplified in Figure 1, grammatical class information is automatically and necessarily retrieved whenever a word is comprehended or produced (e.g., Levelt, 1989; Pickering and Branigan, 1998): because grammatical class information must be always retrieved during sentence processing, and because language use predominantly requires connected speech, rather than production of words in isolation, this information would always be activated during processing even of single words. Such a view leads to the prediction that grammatical class effects should be found whether words are comprehended or produced, and whether they appear in isolation or in sentence context. A weaker version assumes, instead, that grammatical class information, although lexically represented, is only activated when necessary, namely when sentences are produced or understood and not when processing single words (e.g., Levelt et al., 1999).

In the second class of theoretical proposals, which we refer to as *combinatorial* views, grammatical class, like other morpho-syntactic information, is not considered to be lexically specified (and hence retrieved from memory), but rather, to be part of combinatorial/integration processes that apply to words during the processing of sentences (e.g., Garrett, 1976, 1984; Ullman et al., 1997). The manner in which these combinatorial operations have been described in the literature varies from strictly syntactic operations (based on phrase structure grammar, X-bar theory, etc., e.g., Garrett, 1984) to a more general distinction between declarative (lexical) and procedural (integrative) knowledge (e.g., Ullman et al., 1997). Critically, all these views assume that grammatical class would only be relevant to processes of integration, and that it would be processed by a system clearly distinguishable from the one used for lexical retrieval. A number of these psycholinguistic theories are grounded in *Generativist* approaches in linguistics (e.g. Baker, 2003; McCawley, 1998). These approaches aim at finding universally applicable definitions of grammatical categories, including of nouns and verbs. According to generative linguistics, meaning alone does not distinguish between the lexical categories, because nouns, verbs and adjectives can express similar meanings. The crucial differences among them are syntactic and/or morphological. Grammatical categories are defined by the positions they take up in a sentence in relation to other grammatical categories, and by the inflectional and derivational affixation they take.

Finally, in *emergentist* views, grammatical class information is neither part of our lexical nor procedural knowledge, but rather a property emerging from a combination of constraints: most importantly, semantic constraints—the fact that prototypical nouns refer to objects and prototypical verbs refer to events; co-occurrences in speech (namely the fact that nouns and verbs tend, statistically, to co-occur with different types of words around them, Elman, 2004; Burgess and Lund, 1997); other language specific patterns of marking that are regularly applied to one or the other grammat-

ical class (Croft, 2001) and finally phonological typicality, namely the fact that subtle phonological regularities exist between noun or verb classes (Farmer et al., 2006; Kelly, 1992; Monaghan et al., 2005). Each of these constraints by itself may not allow one to classify all nouns and verbs correctly in a given language, however, when taken together their statistical power is greatly enhanced. For example, Elman (2004) discusses how simple recurrent networks can learn to predict, in a probabilistic manner, grammatical properties of words, and can categorize words according to their grammatical class simply on the basis of semantic and contextual constraints. These constraints will give rise to building expectations for the upcoming word in comprehension and in increasing the probability of retrieving either a noun or a verb in production. Thus, effects of grammatical class would come about only when words are used in context, and when the context sufficiently biases the probability for a noun or a verb to occur. Emergentist views of processing align with *Functionalist* and *Cognitive* Linguistic proposals (Sapir, 1921; Givón, 1984; Langacker, 1987; Croft, 1991) suggesting that lexical categories are prototype notions with fuzzy boundaries, grounded in semantic and pragmatic dimensions. According to this perspective, verbs denote events which are dynamic, and short-term states of affairs, while nouns denote states or properties, which are long-term affairs; nouns are prototypical referring expressions while verbs are prototypical predicative expressions. A more detailed description of how these types of theories can deal with cross-linguistic variation will be provided in the discussion.

To summarise, it is unquestionable that the distinction between grammatical categories in general, and between nouns and verbs in particular must become available in one way or another to speakers of a language. The cognitive models described above differ with respect to: (a) *when* grammatical class information becomes available during processing (according to a strong lexicalist view this information is always available, whereas for the other models it is available only when sentences are processed). (b) Whether *knowledge* of grammatical class is required (according to the emergentist view and some versions of combinatorial views, grammatical knowledge is not required, it is required by the other models which differ with respect to whether this knowledge is stored in the lexicon–as the lexicalist views, or instead it is procedural). (c) Whether grammatical class can be defined independently from semantic distinctions, as assumed by lexicalist and combinatorial views, or whether instead semantic distinctions are foundational to grammatical class, as in the emergentist view.

1.2. Neural models

In terms of neuroanatomical models, three main views have been put forward in the literature that bear some correspondence to the three cognitive architectures described above. The first hypothesis, motivated on the basis of neuropsychological data, has been that nouns and verbs are represented in at least partially separable neural networks, with noun processing engaging left temporal areas and verb processing engaging left inferior frontal areas (e.g., Damasio and Tranel, 1993; Daniele et al., 1994). Such a view implies that the networks engaged by processing words from different conceptual domains (objects and actions) would further be fractionated to distinguish grammatical class of words. Such a hypothesis goes hand in hand with a strong lexicalist view. Critical tests of this hypothesis are experiments that control for the correlated semantic difference between objects and actions as well as the different processing demands for nouns and verbs, and that use words in their citation form.

A second possibility represented in the literature is that it is not nouns and verbs *per se* that are processed in partially distinct neural networks, but rather the morpho-syntactic processes that apply to nouns and verbs that are computed in partially separate networks. In the work by Shapiro et al. (2006), it is suggested, for example, that whereas left temporal (including fusiform) areas are engaged by processes that integrate nouns into phrases, left inferior and especially middle frontal areas are specifically engaged by processes that integrate verbs into phrases. The underlying logic here is that morpho-syntactic processes that apply to words from these different grammatical classes would be computed by neural networks in close physical proximity to the networks engaged by the semantic content of words. With respect to cognitive architecture, this neural model is compatible with weak lexicalist views, and with combinatorial views that distinguish syntactic processes related to nouns and verbs, given that according to both we should observe differences between noun and verb processing (and in the corresponding neural systems) only when sentences are produced/comprehended, once semantic correlates and processing demands are controlled. This neural hypothesis is not compatible, however, with those combinatorial views that simply pose a distinction between lexical and procedural processes and with emergentist views, because they both imply a common neural system underlying the morpho-syntactic processing of nouns and verbs. Critical evidence in favour of this view would consist in finding differences between nouns and verbs once the semantic correlates, as well as processing demands, are controlled in tasks that involve phrases/sentences but not single words.

The final hypothesis is one in which no neural separability is assumed for words of different grammatical classes; rather neural separability is assumed for words referring to actions vs. words referring to objects (regardless of their grammatical class). The same shared neural network would be engaged in integration processes for both nouns and verbs. The extent to which such a network would be engaged would depend upon the processing complexity/demands of the task (e.g., Siri et al., 2008) or by the types of morpho-syntactic processes (Tyler and Marslen-Wilson, 2008). This final hypothesis is compatible with those combinatorial views that do not assume specialised processes for words from different grammatical classes and emergentist cognitive architectures. Tyler and Marslen-Wilson (2008), for example present an explicit version of a combinatorial view in which they make a clear distinction between accessing lexico-semantic information mediated by bilateral temporal lobe structures (especially superior and middle temporal gyrus) and a left lateralised (human-specific) system primarily involving superior temporal and inferior frontal areas devoted to computing morpho-syntactic operations that apply to words from different grammatical classes. Emergentist views predict that the neural systems engaged depend upon the statistical weight of specific constraints with semantics/pragmatics playing the main role. Thus, partly specialized networks will be engaged in processing words referring to objects and actions (regardless of whether they are nouns or verbs). In addition, whether other cues such as co-occurrence and phonological typicality follow statically consistent patterns may engage inferior frontal areas, responsive to differences in processing demands, to different extents. Critical evidence would consist in finding strong effects of manipulation of semantic properties of words and of processing demands, in the absence of any effect of grammatical class (once the correlated semantic distinction between objects and actions is controlled). Fig. 2 provides a schematic summary of these three hypotheses.

2. Behavioural studies

Only a small number of behavioural studies have assessed grammatical class effects in language comprehension and production. In the 1990s a number of comprehension studies assessed processing differences between nouns and verbs, presented as single words without sentence context to the left or right visual field. For exam-

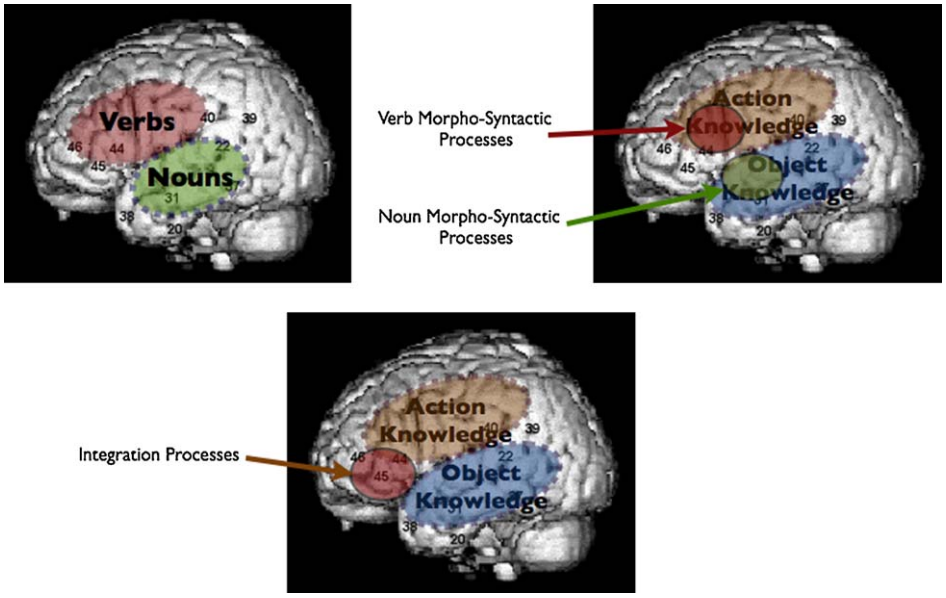

Fig. 2. Schematic overview of different neural models concerning the processing of nouns and verbs.

ple, Sereno (1999) compared nouns and verbs presented to either to the left or right visual fields and asked participants to perform lexical decision or a noun/verb classification task. In both tasks nouns elicited faster responses than verbs overall, and there was a hemispheric difference for verbs (faster responses when verbs were presented in the right visual field) but no such difference for nouns. Grammatical class differences by visual field in lexical decision were also reported by Day (1979), who found right visual field advantages for all verbs, but only for low-imageability nouns. Finally, Nieto et al. (1999) also found grammatical class differences by visual fields (within a complex pattern of results, which also differed by participant gender). However, none of these differences can be unambiguously attributed to grammatical class as all these studies confounded grammatical class and semantics, by using nouns referring to objects and verbs referring to actions. Chiarello et al. (2002) attempted to lessen the confounding effect of semantics by controlling for imageability, a variable that correlates with the distinction between objects and actions/events, as objects typically tend to be more imageable than events. They found consistent visual field effects (processing advantage for right visual field presentation, hence for the left hemisphere) for both nouns and verbs. Nouns were also no faster than verbs overall, in contrast to previous studies. These results seem to indicate that grammatical class may not play a role in the recognition of single words, once semantic correlates are controlled for.

A reliable effect of grammatical class in comprehension, however, has been systematically reported in sentential contexts, a finding that is accounted for by all cognitive theories. For example, early investigations using word-by-word visual presentation of partial sentences have found that speakers are faster in making a lexical decision on a subsequently-presented target word when its grammatical class is consistent with the previous context than when it is not (Wright and Garrett, 1984). This is the case even when the target word is semantically anomalous in context.

More critical to distinguishing between theoretical views are studies that compare processing of single words and processing of words in context. Vigliocco et al. (2008) assessed priming effects in a lexical decision task for nouns and verbs. In the first experiment, semantic control was achieved by using only nouns and verbs referring to events as targets and primes. Primes were either nouns or verbs, while targets were always verbs. A second experiment employed semantically unrelated noun and verb primes, again with verb targets. Crucially, verb primes facilitated recognition of (verb) targets, but only when prime words were inserted in a phrasal context (nouns presented with "the", or verbs presented with "to") and not when they were presented as bare words, a result that goes against strong lexicalist views.

Moving from comprehension to production, it has been often observed that speakers are faster in naming pictures of objects than pictures of actions (e.g., Vigliocco et al., 2004). However, again, such a difference can be accounted for in terms of semantic differences between objects and actions, rather than in terms of differences between nouns and verbs. A number of studies more directly investigating the role of grammatical class have employed the picture-word interference task, in which participants name a picture whilst ignoring a distracter word. In a number of experiments in German and English (Pechmann and Zerbst, 2002; Pechmann et al., 2004), participants were presented with pictures of objects (e.g. apple), and distracters, which were of the same grammatical class (nouns, e.g. "balloon") or different grammatical class (words like "anyhow", "seldom", "forever"). When participants named the pictures as single words, the distracters' grammatical class had no effect, but when participants were asked to produce the same picture names in sentence contexts (such as "Peter beschreibt. . ." [Peter describes. . .]) or in a phrase contexts ("the" + noun), naming latencies were slower for noun distracters than distracters of a different grammatical class. In contrast to comprehension, in a production task this effect is inhibitory in nature, which might be attributed to lexical competition whereby the distracter word would compete with the target word in being assigned to the sentential frame (Kempen and Hoenkamp, 1987), but only in cases in which phrases or sentences are being produced.

Effects of grammatical class in sentence production are also well documented in speech errors; all types of word substitution and exchange errors are strongly influenced by the grammatical class of the intended word (Fay and Cutler, 1977; Garrett, 1975, 1980), indicating that grammatical class has a robust and widespread influence in connected speech. Such results, however, demonstrate grammatical class effects only in sentence processing, and offer no way to discriminate between effects of semantic and grammatical class. For example, when considering semantically related word substitution errors such as mistakenly saying "dog" when "cat" is intended, the fact that they share grammatical class may just derive

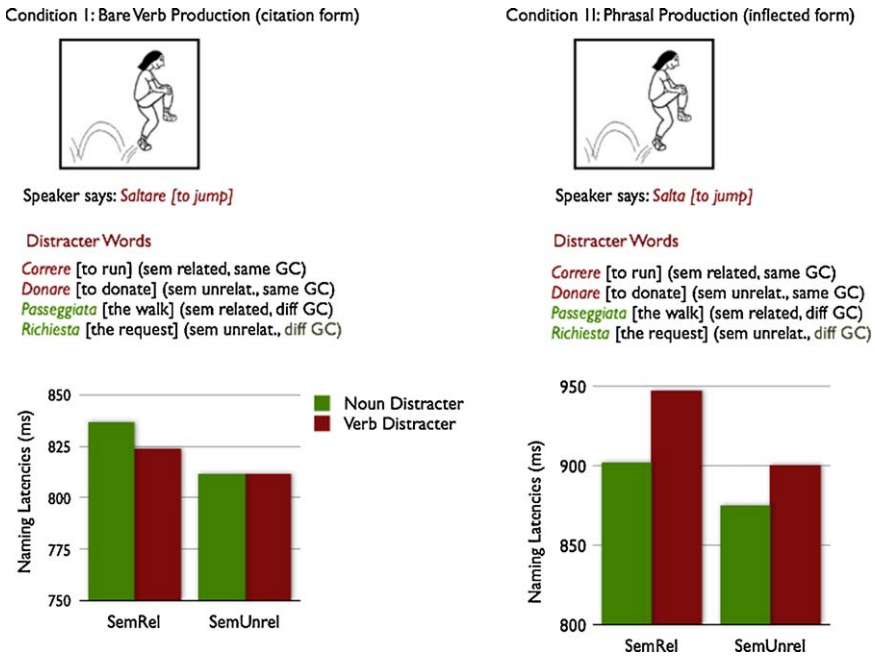

Fig. 3. Illustration of methods and Results of Vigliocco et al. (2005). Italian speakers named pictures of actions using either a bare verb (citation form, appearing in the left panels), or a third-person inflected form of the verb (appearing in the right panels).

from the fact that the semantic neighbourhood of "cat" is made up only of nouns (referring to animals).

In a series of cross-linguistic studies, Vigliocco and colleagues have assessed whether grammatical class effects can be observed for single words and words in sentence context in languages that differ concerning how grammatical class is morpho-syntactically realized and hence in their processing demands. They found that once semantic correlates of grammatical class are controlled (by using only words referring to events, either nouns or verbs), grammatical class only exerts an effect on production when speakers produce phrases and not when they produce single words and only in some but not other languages (Vigliocco et al., 2005; Iwasaki et al., 2008).

Vigliocco et al. (2005) used the picture-word interference paradigm. Italian speakers were instructed to name a target picture using a verb in bare (citation) form, or using a verb form inflected for the third person, singular and present tense. This form of the verb can be considered as a sentence fragment because the subject may be omitted in Italian, being a pro-drop language. A distracter word, presented either above or below the target picture (all referring to events), was semantically related or unrelated to the target, and was either a noun or a verb. Whereas a reliable semantic interference effect was found in both naming conditions (speakers were slower at naming the target when semantically related distracters were presented, compared to semantically unrelated distracters), the distracter word's grammatical class affected the processing of the target verb only when it was produced in the inflected form, not in the citation form. Moreover, the semantic and grammatical class effects did not statistically interact. Examples of items and results are presented in Fig. 3.

Interestingly, in a similar study of action naming in Japanese, in which participants were asked to name action pictures using verbs, either as single words or in sentence contexts, no grammatical class effects at all were observed (Iwasaki et al., 2008), in contrast to the study of Italian by Vigliocco et al. (2005). This difference can be accounted for in terms of cross-linguistic differences between Italian and Japanese. In Italian, the verb needs to agree (in person and number) with the noun, subject of the sentence but this is not the case in Japanese, thus making the task of producing verbs in Italian sentences more demanding, more reliant on distributional cues than in Japanese sentences (see Iwasaki et al., 2008 for an extensive discussion).

Another relevant study in this regard suggests instead that the role of grammatical class in the picture-word interference paradigm is even more restricted. Janssen et al. (in press) found that imageability, rather than grammatical class, affected naming latencies even in sentence contexts (as in the studies by Pechmann and colleagues).

The conclusion that we can draw from these behavioural studies is that grammatical class information is not a lexical property that is automatically and necessarily retrieved when retrieving single words, but a property that can play a role in sentence context. Critically, the role that grammatical class plays in sentence processing is modulated by cross-linguistic differences in how words from different grammatical classes are used in sentences. In terms of the cognitive models we have sketched above, these results are more easily accounted for in combinatorial and emergentist, rather than in lexicalist views because the lack of an effect in single word production across languages combined with the finding of cross-linguistic differences at sentence level cannot be accounted for by either strong or weak versions of lexicalist hypotheses.

3. Electrophysiological studies

Event Related Potentials (ERPs) have been widely used in the study of language processing, including the grammatical class distinction (for reviews see Kutas et al., 2006; Barber and Kutas, 2007). In a pioneering study, Neville et al. (1991) found that the substitution of a word for another of different grammatical class resulted in an early left frontal effect (N125), followed by a more posterior effect between 300 and 500 ms. The early effect, also referred to as Early Left Anterior Negativity (ELAN), has been since found with different phrase structure violations, in different languages, and both with auditory and in visual presentation (Osterhout and Holcomb, 1992, 1993; Munte et al., 1993; Friederici et al., 1993, 1996). As in Neville et al's study, it has been shown that the ELAN has an earlier latency (100–250 ms) than other ERP components which show the same scalp distribution (between 300 and 500 ms),

and are associated with the processing of other syntactic violations (Osterhout and Holcomb, 1993; Rösler et al., 1993; Gunter et al., 1997; Coulson et al., 1998; Barber and Carreiras, 2005). It has been proposed that the ELAN could reflect initial syntactic processing based only on grammatical class information (Frazier and Fodor, 1978; Frazier, 1987; Friederici, 1995; Friederici et al., 1996; Hahne and Friederici, 1999). However, other authors have interpreted LAN effects (regardless of latency) simply as an index of working memory processes (Kluender and Kutas, 1993; King and Kutas, 1995).

Other studies have addressed the issue of grammatical class by comparing the processing of open (e.g., nouns, verbs, adjectives) and closed (e.g., determiners, pronouns, conjunctions) class words during comprehension of correct sentences. This comparison gives rise to a negativity (N280) in left anterior sites. It is an open question, however, the extent to which this negativity is specific to closed class words (Neville et al., 1992; Nobre and McCarthy, 1994) or not (King and Kutas, 1998; see also Osterhout et al., 1997, 2002; Münte et al., 2001). Just as for the behavioural studies, cross-linguistic differences may also play a role. Brown and colleagues (Brown et al., 1999) in Dutch observed early differences between open- and closed-class words after controlling length and lexical frequency, and showed that this effect is absent in Broca aphasic patients (Ter Keurs et al., 1999, 2002) suggesting that these early negativity indexes quick availability of grammatical class information.

Other studies have addressed the question of whether different cell assemblies may underscore the processing of nouns and verbs during sentence or text processing indicating that cross-linguistic differences in grammatical class ambiguity (i.e., whether the same word form can be used as a noun and a verb) may modulate these effects. In languages such as English, a very large number of words can be used as both nouns and verbs, so their grammatical class depends on the context, this is not the case in highly inflected languages, such as Italian, Dutch or German. In English, no differences were observed in a study where participants read correct sentences (Osterhout et al., 1997). However, in Dutch, Brown et al. (1999) found amplitude differences in the early frontal negativity (peaking at 312 ms post-stimulus-onset), with more negativity to verbs than to nouns and a similar difference (with the same polarity but larger at posterior electrodes) in a later (between 350 and 500 ms) window. Federmeier et al. (2000) compared the ERP waveforms of grammatical class ambiguous words (could be either verbs or nouns), with those of unambiguous verbs and nouns in a sentence context. In order to reduce semantic confounding, they selected nouns and verbs from semantic domains not restricted to objects and actions. Responses to nouns, regardless of grammatical class ambiguity, were more negative than those to verbs between 250 and 450 ms over central–posterior sites. Verbs and nouns also showed a frontal negativity with an onset of approximately 150 ms, but only if they were unambiguous with respect to grammatical class. Finally, in comparison with unambiguous words, class ambiguous words elicited a slow, frontal negativity starting from about 200 ms after word onset. These effects were mainly replicated in a later study in which nouns and verbs were presented in minimal phrases: nouns preceded by "the", and verbs preceded by "to" (Lee and Federmeier, 2006). Therefore, ERP measures to words presented in context seem to be sensitive to the grammatical distinction between nouns and verbs, with differences across languages possibly linked to differences in word class ambiguity.

When we move from studies investigating integration processes of words in context to studies assessing effects of grammatical class on single word retrieval and representation, the studies are far less converging. In the context of pairs and triads of German words, N400 effects associated with semantic priming were found not to be affected by grammatical class, but differences between ERPs evoked by nouns and verbs supported the idea that access to these two types of items involves cell assemblies that are topographically distinct (Khader et al., 2003; see also Rösler et al., 2001). However, a similar study in English reported latency differences in the N400 component of nouns and verbs, but not topographical changes in the distribution of the associated priming effects (Gomes et al., 1997).

Koenig and Lehmann (1996) studied ERP brain fields associated with visually presented German nouns and verbs. Spatial microstate analysis was applied to series of maps obtained from the activity associated with words from both grammatical classes. Nouns' maps differed from verbs' maps between 116 and 172 ms, suggesting different neural generators for the processing of nouns and verbs. Similar results were obtained in studies looking at high frequency electrocortical response revealing differences between nouns and verbs in the 30 Hz range (Pulvermüller et al., 1996, 1999a,b). However, because nouns referred to objects and verbs referred to actions, these differences could be semantic in nature. Pulvermüller et al. (1999a,b) compared three different lists of German words: action verbs, nouns with strong action associations, and nouns with strong visual associations, and performed a Current Source Density (CSD) analysis of the ERPs. Results showed topographic differences depending on grammatical class between 120 and 220 ms after the averaged recognition point of the auditorily presented words. Critically, however, differences between visual nouns and action verbs were similar to those between both types of nouns, and no differences emerged between action nouns and action verbs, thus suggesting an effect of semantics, rather than grammatical class.

ERP amplitude analyses to single words have also shown differences between nouns and verbs, however, again it is unclear whether these differences (when found) are related to grammatical class or semantics. For example, a study showed a modulation of the P200 component at frontal and central sites, with verbs associated to more positive amplitudes than nouns (Preissl et al., 1995; see also Pulvermüller et al., 1999a,b). In a similar experiment with visual single word presentation in Dutch, Kellenbach et al. (2002) compared nouns and verbs that were classified depending on their semantic features: abstract words, words with visual and motor features (e.g. manipulable objects and actions), and words with only visual features (e.g. non-manipulable objects). ERP comparisons showed differences depending on both grammatical and semantic class in the time windows of the P2 and N400 components and no interaction between the semantic and grammatical class manipulation, suggesting independence between the two variables. However, and again, nouns tended to refer to objects and verbs to events, thus including the semantic confound.

In a study carried out in Italian, Barber et al. (in press), minimised systematic correlations between object-nouns and action-verbs by using nouns and verbs referring only to events (e.g., *corsa* [the run]; *correre* [to run]). As in an imaging study (Vigliocco et al., 2006, described in the following section), in addition to manipulating the grammatical class of the words, they further manipulated whether the words referred to sensation (e.g., *odore* [smell-N]; *annusano* [sniff-V]) or motion (e.g., *piroetta* [pirouette-N]; *scalano* [hike-V]). They found that both grammatical class and semantic attributes showed the same ERP effects: waveforms differed between 300 and 450 ms after word onset at posterior electrode sites, with the amplitude values associated with nouns and sensory words being more negative than those of verbs and motor words respectively. These effects had a centro-parietal distribution with no clear lateralisation, and were interpreted as a modulation of the N400 component. The N400 component has been related to semantic processing, and it has been suggested that it is a good index of the ease of accessing information within long-term semantic mem-

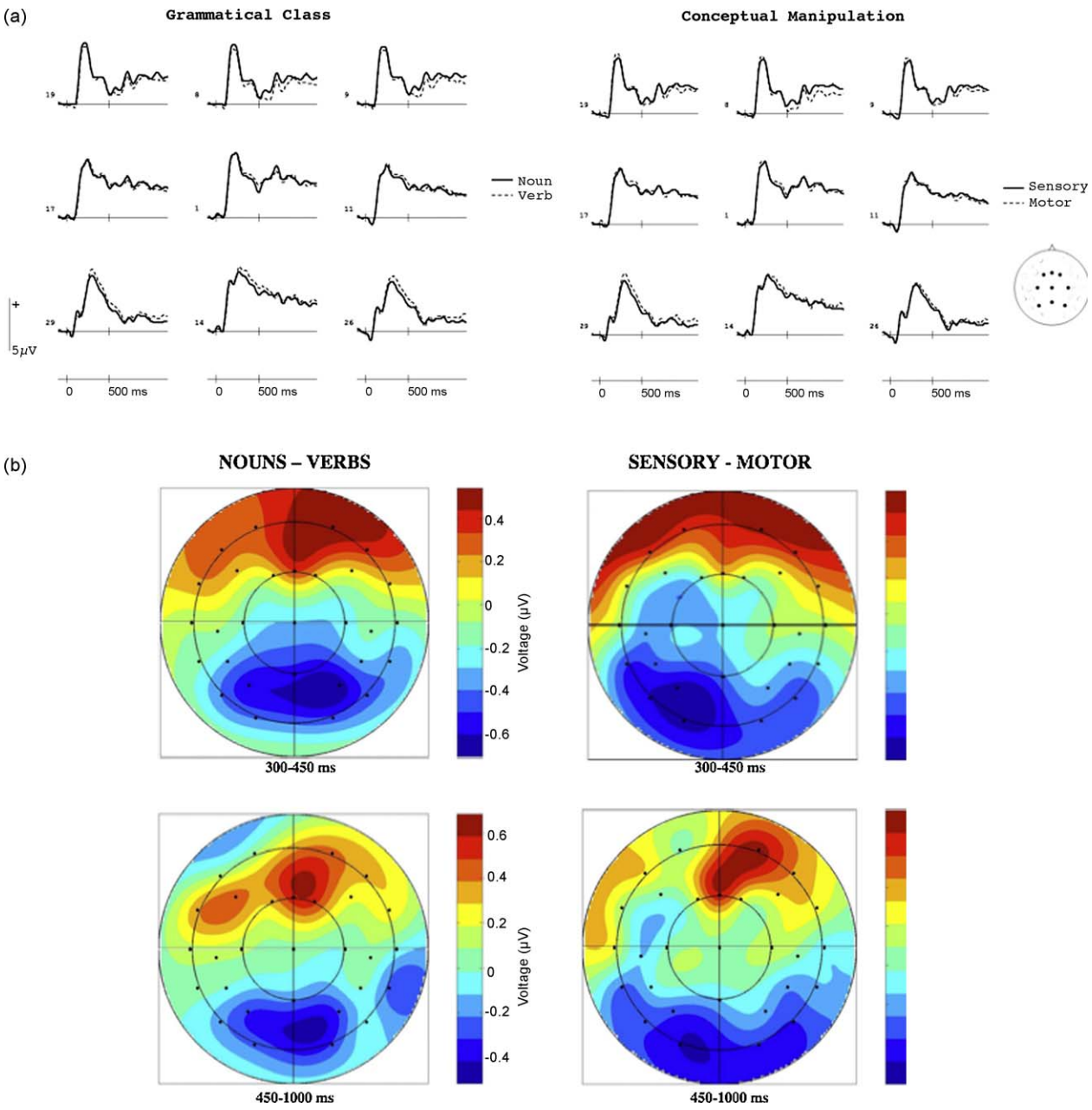

Fig. 4. Grand averages (a), and topographical distribution (b) for the grammatical class (nouns vs. verbs) and semantic manipulations (sensory vs. motor) in processing of single words (Barber et al., in press).

ory (Kutas and Federmeier, 2000; Molinaro et al., in press). This way, the N400 amplitude is sensitive to (amongst others lexical and contextual variables) semantic attributes of the words; it is modulated at frontal electrodes by word concreteness (Kounios and Holcomb, 1994), and changes its distribution when different semantic networks are activated, for example those related with animal names or tool names (Kiefer, 2001, 2005; Sitnikova et al., 2006). Importantly, the study of Barber et al. (in press), showed that once semantic confounds are minimised, electrophysiological data do not show qualitative differences in the responses to nouns and verbs, at least when only lexical retrieval processes are engaged in single word processing (even in a morphologically rich language such as Italian). The N400 amplitude differences associated to motor and sensory features of the words, and to the nouns and verbs comparison did not differ in terms of latency, duration or scalp distribution (see Fig. 4), consistently with the proposal of a single neuronal generator for both semantic and grammatical class effects, which ultimately would be semantic in nature.

4. Neuropsychological studies

In contrast to the relatively sparse behavioural and EEG literature on noun–verb processing, there is a wealth of reports of patients with focal (e.g., Aggujaro et al., 2006; Bastiaanse and Jonkers, 1998; Berndt et al., 1997a,b; Breedin and Martin, 1996; Hillis and Caramazza, 1995; Kim and Thompson, 2000; Laiacona and Caramazza, 2004; Luzzatti et al., 2002; McCarthy and Warrington, 1985; Miceli et al., 1984, 1988; Shapiro and Caramazza, 2003a,b; Silveri and Di Betta, 1997; Zingeser and Berndt, 1988; Zingeser and Berndt, 1990) and progressive brain damage (e.g., Cappa et al., 1998; Damasio and Tranel, 1993; Daniele et al., 1994; Kim and Thompson, 2004; Parris and Weekes, 2001; Robinson et al.,

1999) showing a dissociation between nouns and verbs. Limiting their review to focal cases that were tested using picture naming, Mätzig et al. (2009) reported that between 1984 and 2006, 240 patients (showing relative impairment of nouns or verbs) were described in 38 papers.

Historically, the double dissociation between nouns and verbs originated in the contrast between agrammatic Broca's aphasic patients whose connected speech often includes only a few verbs, and anomics who have severe word-finding difficulties for (concrete) nouns. Initially, the greater difficulty of Broca's patients with verbs was interpreted in terms of the greater syntactic complexity of verbs in comparison to nouns (e.g., Saffran et al., 1980; Saffran, 1982). However, the argument that verbs are broadly more difficult to produce was undermined by studies showing that anomic patients produce verbs more readily than nouns (e.g., Miceli et al., 1984, 1988; Zingeser and Berndt, 1988).

The vast majority of subsequent research focused on picture naming, and differences between object and action naming in Broca's aphasic and anomic patients were conceptualized as a double dissociation. Such double dissociation related to noun–verb differences seems to encompass: (1) selective noun or verb deficits, (2) contrast between agrammatic and anomic patients, and (3) contrast between frontal and temporal lobe lesions. Thus, agrammatic Broca's aphasics are expected to have lesion in the frontal lobe and verb deficits, and anomics, lesion in the temporal lobe and noun deficits. By inference, frontal lobe regions became associated with verb processing and temporal lobe regions with noun processing.

One first problem in interpreting selective deficits in noun or verb processing is that the magnitude of the dissociation between nouns and verbs is extremely variable (in Mätzig et al.'s review, the differences ranged between 2 and 81%). Moreover, many more patients are reported with verb deficits than noun deficits (of the 240 patients reviewed, 11% presented with noun and 75% with relative verb deficits). This latter would not be a problem *per se*, however, there is also evidence that neurologically intact young and elderly participants find action naming more difficult than object naming, both in terms of accuracy and of latencies (Bogka et al., 2003; Druks et al., 2006; Szekely et al., 2005). Thus, it is rather plausible that at least some of the verb impairment cases (those with relatively small differences between the processing of nouns and verbs) are due to action naming being inherently more difficult than object naming.

The most critical problem with most neuropsychological studies, however, is that picture naming is used to assess the relative impairment of noun–verb processing, hence once again, grammatical class is inherently confounded with semantics. There is in fact evidence suggesting a clear association between left temporal lesions and object naming deficits, and left frontal lesions and action naming deficits (Tranel et al., 1997). In a first attempt to disentangle semantics and grammatical class, Berndt et al. (2002) supplemented picture naming data with sentence completion data with abstract nouns and verbs. They found that five patients showing relative verb impairment in picture naming were also disproportionately impaired on verbs in sentence completion in which the last word, either a noun or a verb (a highly probable completion of the sentence) was missing. The advantage of this study over picture naming is that by using abstract nouns and verbs it lessens the semantic confound between grammatical class and objects/actions. Moreover, it allows one to assess the correlation between performance when using words in isolation and in sentences. A problem, however, is that no patients with relative noun deficits were tested to see if they would present with the reverse pattern. These participants would have been essential to support Berndt's et al. claim that their data indeed constitute evidence for the double dissociation between nouns and verbs as related to grammatical class beyond semantic differences between object and action knowledge. Moreover, the correlation between noun or verb-specific deficit in picture naming and in connected speech has not been found in other studies (Druks and Carroll, 2005; Mätzig et al., 2009).

An alternative way to attempt to disentangle semantics and grammatical class has been to assess patients' performance in tasks using pseudonouns and pseudoverbs, in addition to real nouns and verbs. The underlying logic is that if a patient shows an impairment with real verbs and pseudoverbs (or nouns and pseudonouns) the deficit cannot be semantic in nature, because pseudowords do not have meaning. Shapiro and Caramazza (2003c) used a morphological transformation task in which participants were asked to change singular nouns to plural, and present tense verbs to past tense, or vice versa, within a short sentential context (e.g., *a wug* → *many wugs*; *he wugs* → *they wug*). It was found that patient RC (Shapiro and Caramazza, 2003) was impaired in action naming and in inflecting verbs as well as pseudoverbs; whereas patient JR (Shapiro et al., 2000) was more impaired in object naming and in producing inflected nouns and pseudonouns. Laiacona and Caramazza (2004) have argued that these results could be accounted for by assuming that the lexicon is organised according to grammatical class. However, such an account cannot explain why the patients also have problems with the pseudowords, given that these latter do not have a lexical representation. Most important, the underlying logic according to which pseudonouns and pseudoverbs do not engage semantics is problematic. It is plausible, in fact, that speakers do interpret these pseudowords by assigning them some kind of meaning, and that the meaning they assign them is biased by the specific sentence context in which the pseudowords are presented, namely pseudonouns, being introduced by a determiner or quantifier ("a", "many") are interpreted as object-like; whereas pseudoverbs being introduced by a pronoun ("s/he" or "they") are interpreted as action-like.

To evaluate this possibility, we have carried out the following small-scale experiment. During a first phase, we asked a group of six native English speakers to guess what each of forty pseudowords (e.g., "wug") meant, presenting them in context (*a wug*, *many wugs*, *he wugs*, *they wug*). Each subject saw a given pseudoword in only one context, and 10 pseudowords for each context. In the second phase, we presented the definitions provided by these speakers (240 definitions) to an additional group of ten native English speakers. These speakers were asked to guess whether the definition referred to an object, an action, an abstract concept or something else. Pseudowords presented in a "noun" context (e.g., *a wug*/*many wugs*) were judged to refer to objects 84% of the time (e.g. *a wug*: "furry animal from South America"); pseudowords presented in "verb" context were judged to refer to actions about 83% of the time (e.g. *they wug*: "to squirm"), thus indicating that pseudowords were semantically interpreted as object/noun or action/verb depending upon the sentence context in which they were presented. Thus, the contrasting performance displayed by JR and RC does not unequivocally demonstrate selective impairment for noun or verb processing. The observed double dissociation between the two patients may be explained simply in semantic terms and further underscoring the foundational role of semantic/pragmatic distinctions to grammatical class membership.

Getting back to the general finding of dissociations in patients' performance in naming object and action pictures, impaired naming may come about for different reasons. More specifically, whereas selective impairment of object-noun naming could come about only as a consequence of semantic impairment; action-verb deficits may come about as a consequence of different types of impairment, not just a semantic impairment because, as we have discussed earlier, verb processing is more demanding than noun processing. This would explain why verb impairments are more commonly observed than noun impairments. Moreover, there

Table 1
Lesion data for patients with selective noun-deficit, and verb-deficit (summary of Table 4 in Mätzig et al., 2009; reference information provided in Mätzig et al., 2009).

Lesion site	Number of patients
Noun naming < verb naming	
L. Fronto-Temporal	1
L. Temporo-Parietal (Bilateral)	2
L. Fronto-Temporo-Parietal	1
L. Temporo-Parietal-Occipital	2
L. Temporo-Occipital	2
L. Temporal	4
Verb naming < noun naming	
L. IFG, premotor, Insula, Internal Capsule	1
L. IFG, White Matter	1
L. Internal Capsule, White Matter	1
L. Basal Ganglia	1
L. Parietal, White Matter, External Capsule, Thalamus	1
L. Insula, Basal Ganglia, External Capsule, Thalamus	3
L. Fronto-Temporal	4
R. Fronto-Temporal	1
L. Occipito-Parietal	1
L. Temporo-Parietal	3
L. Fronto-Temporo-Parietal	3
L. Temporal	1
L. Parietal	3

would be far less consistency in lesions among patients with verb than noun impairments. This has been reported by Mätzig et al. and is summarised in Table 1. The data reported are the lesion sites for 36 patients who show a large (>30%) noun–verb difference, 12 with noun and 24 with verb deficits. The spread of the lesions tends to be posterior and the temporal lobe is always involved in disproportionate noun deficits. In contrast, the spread of the lesions in verb deficit is more disparate, and the frontal lobe is not always involved.

To summarise, the large body of evidence from focal lesion studies does not allow one to conclude that grammatical class is an organisational principle of lexical knowledge in the brain. Picture naming studies suggest that for nouns, indeed the deficit may well come about as a consequence of lesions affecting the network involved in the representation of object knowledge (with lesions involving left inferior temporal regions). For verbs, the deficit can be linked to different causes: impairments of the network engaged in processing action knowledge (frontoparietal) and/or impairments of other processes, possibly dependent upon executive functions, that impose greater demands on verbs than nouns.

In addition to focal lesion studies, a number of investigations have assessed the impact of degenerative brain disorders in frontotemporal dementia and Alzheimer's disease on noun and verb processing. The rationale for these studies is anatomical. Since the different neuropathological varieties of dementia affect different brain regions in their early stages, noun–verb differences may be expected to occur on the basis of the findings from focal lesion studies. In particular, early Alzheimer's disease is centred on the temporal lobe, and hence should affect noun processing more than verb processing. The reverse pattern should be observed in frontotemporal dementia (FTD), which mainly affects the frontal lobe and only the anterior portion of the temporal lobe. As in the case of focal lesions, most of the studies have been based on object and action naming and comprehension tasks, thus confounding the semantic and the grammatical class distinction.

In the first study comparing object and action naming performance of AD and FTD patients, Cappa et al. (1998) found that, while both FTD and AD groups were impaired in naming, action naming was significantly worse than object naming in FTD than in AD patients, independently of the severity of dementia or of overall language impairment. In another study, Rhee et al. (2001) reported that FTD patients were also significantly less accurate and required significantly longer response times to make word-picture matching decisions about verbs compared to nouns. In subsequent studies it became clear that is important to separate the contribution of the different varieties of FTD to the reported verb naming impairment. It is now established that the clinical label encompasses a number of heterogeneous clinical presentations, in which different patterns of neuropsychological impairments in linguistic processing, executive function and action organisation reflect the localisation of the underlying pathology (Josephs, 2008), and may affect verb processing in different ways.

A systematic investigation of object and action naming and comprehension in a relatively large sample of patients with a clinical diagnosis of FTD was performed by Cotelli et al. (2006), who included all three subtypes of the disorder: the frontal variant (FvFTD), non-fluent primary progressive aphasia (NfPPA) and semantic dementia (SD). Moreover, the study included two other conditions, progressive supranuclear palsy (PSP) and corticobasal degeneration (CBD), which overlap both clinically and neuropathologically with FTD, and are now considered to be part of the same pathological spectrum (for a review, see Josephs, 2008). These two varieties are characterised by prominent movement disorders, and are frequently associated with language impairment. Cotelli et al. (2006) found that, with the exception of SD, verb naming was more impaired than noun naming in all patient groups. However, verb naming was significantly more impaired for patients with NfPPA and PSP than patients with CBD, FvFTD and AD (see Fig. 5). Auditory comprehension of verbs was affected only in FvFTD, SD and AD patients. These findings indicate that the presence of a lexical retrieval disorder, which is particularly severe for verbs, is not typical of FTD in general, but can be found in association to non-fluent progressive aphasia and conditions characterised by prominent movement disorders. Importantly, in this study, the semantic dementia patients, the temporal form of FTD, did not show selective verb sparing. However, using different materials, Robinson et al. (2008) showed that SD patients name action pictures significantly better than object pictures.

Because patients in all these studies were assessed by contrasting object to action naming, a semantic explanation in terms of action naming or action knowledge of this result seems the most plausible. The evidence from SD patients who have focal atrophy in the anterior and inferior temporal lobe provides a strong argument for this account. These patients have no language deficits apart from severe anomia, in the context of severe semantic deficits. Both nouns and verbs are affected, but nouns to a larger extent, likely because object names rely on inferior temporal structures (e.g., Damasio et al., 2004). The likely semantic/conceptual nature of the disorder in the case of CBD patients is further supported by an additional observation from the Cotelli et al. study. The action items in this study were divided into "manipulation actions" and "non-manipulation actions". The CBD patients who have prominent limb apraxia were more severely affected in the naming the manipulation actions than in naming the non-manipulation actions. Even more striking are the results of a study with patients affected by motor neuron disease. Confirming previous case studies of MND disease patients showing verb naming impairment, Grossman et al. (2008) reported defective action knowledge in this disease, which was correlated to cortical atrophy involving the motor cortex.

Just as for the focal lesion studies, it is well-documented that verb deficits may also come about for non-semantic reasons. Rhee et al. (2001) found a correlation between executive dysfunction, assessed with tests such as the *Stroop* and *Trail Making*, and defective verb comprehension only in patients with the frontal variant of FTD. Similarly, Silveri et al. (2003) found a stronger correlation between action naming deficit and severity of dementia in the frontal variant than in AD. The correlation analysis also sug-

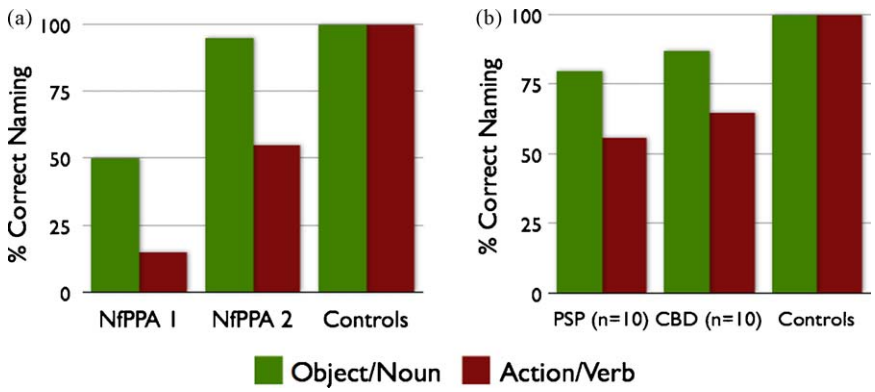

Fig. 5. Object and action naming for two patients suffering from Non-fluent Progressive Primary Aphasia (NfPPA) and matched controls (panel a); groups of Progressive Supranuclear Palsy (PSP) and Corticobasal Degenration (CBD) and matched controls (panel b); data from Cotelli et al. (2006).

gested that the naming disorder was due to a dysexecutive deficit in FTD, and to a linguistic disorder in AD. In the case of non-fluent primary progressive aphasia (NfPPA), which is typically associated with agrammatism, the severe verb naming impairment probably reflects an underlying morphosyntactic disorder (Cotelli et al., 2006). It is noteworthy that in the Rhee et al. study a significant correlation was found with sentence comprehension, further suggesting a more general impairment of sentence integration processes.

To summarise, different mechanisms of impairment, reflecting the anatomical selectivity of the pathological process, may be responsible for defective verb processing in neurodegenerative disorders. Just as we have seen for focal lesion studies, a primary factor responsible for dissociations is semantics: defective action knowledge appears to be a crucial factor in particular in the case of movement disorders. The relative verb sparing in SD has also clear semantic underpinnings as neuropathology does not affect the neural representation of action knowledge. Moreover, the greater processing demands posed by verbs may play an important role as illustrated in studies of groups of AD patients who show poorer performance in verb than in noun naming (Druks et al., 2006; Masterson et al., 2008). Thus, overall, lesion studies do not support the idea (depicted in Figure 2) of neural separability between nouns and verbs.

5. Transcranial magnetic stimulation studies

Repetitive transcranial magnetic stimulation (rTMS) was initially introduced with the idea that it could produce a "virtual lesion" that would allow direct testing of the functional role of a brain area by observing the behavioural consequences of the (transient and reversible) functional inhibition it creates. The actual mechanisms of TMS interference with brain activity are considerably more complex than this, as indicated by the results of what is now a large body of investigation (Devlin and Watkins, 2007). Shapiro et al. (2001) used rTMS to suppress the excitability of a portion of left prefrontal cortex, with the aim to assess its role in producing nouns and verbs. English-speaking subjects were asked to generate the singular or plural of nouns, or the third person singular or plural in the case of verbs. In one experiment participants generated real words, while in a second, they produced pseudowords inflected as nouns or verbs. In both experiments, response latencies increased for verbs and pseudoverbs but were unaffected for nouns following rTMS. Similar results were reported by Cappelletti in a recent replication, which involved regular and irregular verbs (2007). However, as we have discussed above for patients JR and RC (who were tested using the same tasks), the semantic confound is not eliminated by using pseudowords. Additionally as these tasks engage morphosyntactic processes in addition to lexical retrieval processes, it is unclear whether greater interference for verb than noun production may just arise from the greater processing demands for verbs. Hence, these results do not provide evidence for the strong claim that grammatical class is an organisational principle of lexical knowledge. They are however compatible with the claim that grammatical class effects emerge when sentence integration processes are engaged and reflect quantitative differences in the extent that a shared network is engaged.

Cappa et al. (2002) assessed the effects of rTMS applied to the left and right dorsolateral prefrontal cortex during object and action picture naming. An action-specific facilitation effect was found after left-sided stimulation. Oliveri et al. (2004), using single and paired pulse TMS in motor cortex found an action word-specific facilitation, independent of the word's noun–verb status, a result accounted for in terms of interference with action knowledge. Gerfo et al. (2008) applied rTMS to a portion of left prefrontal cortex (middle frontal gyrus; first experiment) and to the primary motor cortex (second experiment). Italian participants carried out the morphological transformation task for nouns referring to manipulable objects or abstract entities and verbs referring to actions or abstract events. In the first experiment they found a selective interference specific for action verbs, without any effects for nouns and verbs referring to abstract entities and events. This result suggests that left middle frontal gyrus is engaged in both retrieval and processing of action knowledge (semantics), and, crucially, in integration processes. As we have discussed before, verbs pose greater processing demands than nouns on integration processes. It is intriguing, however, that differential demands on integration processes *per se* did not determine differences for nouns and verbs, as indicated by the lack of any effect for abstract words. By contrast, in the second experiment, interference was found for both nouns and verbs referring to actions but not for nouns and verbs referring to abstract entities and events. This suggests that primary motor cortex is involved in the semantic representation of actions, and therefore stimulation of this site will affect retrieval of action knowledge, regardless of grammatical class of stimuli. This involvement, however, may occur after lexical access, as indicated in a study by Papeo et al. (2009). Using the technique of TMS facilitation of motor evoked potentials by stimulation of the primary motor cortex, these authors found a specific facilitation effect of action word recognition only at 500 ms, and not at 175 or 300 ms post-stimulus presentation, suggesting post-lexical processing. This result is compatible with the timing reported by Oliveri et al. (2004), but not with the results of Buccino et al. (2005) and with the magnetoencephalographic evidence provided by Pulvermüller et al. (2005). Further studies are clearly needed to settle this important issue.

To summarise, TMS studies support a causal role of primary motor cortex and other portions of prefrontal cortex in the representation of the meaning of words referring to action. This is a very important result that indicates that when words are perceived or produced, speakers cannot help but retrieve non-linguistic information associated to motor control, as is predicted by embodiment theories of semantic representation (e.g., Barsalou et al., 2003) but not by other theories that instead argue that word processing does not require engagement of information pertaining to the motor system (e.g., Levelt, 1989). However, TMS studies do not provide compelling evidence for neural separability of words of different grammatical class because such a conclusion would require finding clear double dissociations between noun–verb specific effects after TMS is applied to different networks. So far, the evidence only indicates a greater engagement of left prefrontal regions (middle frontal gyrus, inferior frontal gyrus) in processing verbs than nouns. Moreover, even limiting our attention to single dissociations, it is important to note, as we will further discuss below when reviewing imaging studies, that the middle frontal gyrus areas stimulated in the studies by Shapiro et al. (2001), Cappelletti et al. (2008) and Gerfo et al. (2008) do not neatly correspond to areas of greater activation for verbs than nouns in imaging studies using the same task.

6. Imaging studies

Just like the studies using different methodologies that we have reviewed above, the majority of the imaging studies did not control for the semantic difference between objects and actions, so that many of the comparisons can be interpreted as related to the "object vs. action" contrast (which is, in fairness, the explicit goal of a number of investigations) rather than the "noun vs. verb" contrast. Also, as in studies using other methodologies, the neural substrate of noun and verb processing has been investigated using (comprehension or production) tasks concerning single words or phrases. As we have already abundantly discussed, this dimension is crucial in distinguishing between hypotheses in which grammatical class is a lexical principle of organisation and hypotheses in which noun–verb differences arise only when morphosyntactic processes are engaged. Finally, again, different languages have been used; cross-linguistic variation may again account for some of the inconsistencies across studies.

Table 2 reports the coordinates of the activations found in experiments in which a verb–noun (or vice versa) contrast has been specifically reported. The studies are organised according to the type of task in which the subjects were engaged. The presence of a large amount of variability is hardly surprising, given the number of potential error sources. The experiments were run at different times (from 1995 onward), using different methods (PET or functional MR) and using a variety of data analysis techniques, as well as variation within task types.

Let us start by considering those studies that used tasks recruiting semantic knowledge (word generation, semantic judgement and picture naming). Here, studies in which the materials confounded the semantic distinction between objects and actions and the grammatical class distinction between nouns and verbs generally found differences for the verb–noun contrast, localized in the left prefrontal cortex (most often in the inferior and middle frontal gyrus) and in the left temporal lobe (most often in the middle and inferior temporal gyrus). Importantly, in those few studies in which semantics was controlled, the temporal lobe difference tends to disappear, and inferior frontal activations are observed only when the task engages morphosyntactic processes across languages such as Hebrew, Italian and English (Palti et al., 2007; Siri et al., 2008; Longe et al., 2007).

Table 2
Coordinates of verb- and noun-specific activations reported in imaging studies, organised according to the task performed.

1. Word generation			
Martin et al. (1995)			
Action words vs. color words			
LIF	−42	12	20
LIF	−43	18	6
LIF	−32	34	0
LMF	−36	4	44
LMF	−34	48	16
LIP	−38	−64	36
LMT	−52	−50	0
LMT	−46	−60	16
RCereb	26	−68	−28
Color words vs. action words			
LMF	−42	18	28
LMF	−38	30	20
LForb	−24	32	−8
LIP	−34	−62	40
LFusif	−46	−46	12
LParahipp	−18	−42	4
RFusif	44	−48	−12
Rthal	6	−28	8
Warburton et al. (1996)			
Verbs vs. nouns			
LIF	−56	16	16
PrecentralSulc	−40	0	48
LSMA	−8	4	60
LIP	−52	−38	32
LITSulc	−56	−52	−4
LTPJunc	−46	−60	20
Nouns vs. verbs			
LACing	−6	38	−4
RSTSulc	30	18	36
RCallosalmarginalSulc	18	10	48
2. Semantic judgement			
Tyler et al. (2001), Exp 2			
Verbs vs. nouns			
LIT	−48	−44	−26
Kable et al. (2002)			
Verbs vs. nouns			
LMT-LMST		Not reported	
Tyler et al. (2003)			
Tool actions vs. tools			
LIF	44	−50	16
	47	−44	32
LIns	−38	12	6
Biological actions vs. animals			
LIF	−50	20	10
LIF	−36	28	−2
LIF	−42	24	18
LMT	−60	−50	2
LMT	−52	−32	−4
Tyler et al. (2004)			
Verbs vs. nouns			
LIF	−50	16	12
LIF	−38	22	0
LIF	−46	22	6
Bedny and Thompson-Schill (2006)			
Verbs vs. nouns			
LPCing	−9	−36	21
LST	−57	−39	15
Nouns vs. verbs			
LIT	−57	−30	−21
Davis et al. (2004)			
Verbs vs. nouns			
LMT	−54	−48	−6
Palti et al. (2007)			
Verbs vs. nouns			
LIF	−47	7	14 sem task only
LPMF	−25	9	51 morph task only
LSTSulc	−54	−36	3 both

Table 2 (*Continued*)

Bedny et al. (2008)			
Action verbs vs. animal nouns			
LST/IP	64	−16	10
Verbs vs. nouns			
LST/IP	−62	−44	20
LIF	−52	22	0
RM/ST	62	−32	2
3. Picture naming			
Damasio et al. (2001)			
Verbs vs. nouns			
LIT	−43	−72	9
RAng	37	−82	31
Tranel et al. (2005)			
Homonymous verbs vs. Nouns			
LMT	−52	−70	9
Non-homonymous verbs vs. nouns			
LMT	−51	−67	6
LMT	−55	−55	6
LFO	−35	19	29
LFO	−50	26	17
LSTS	−46	−35	−3
Saccuman et al. (2006)			
Verbs vs. nouns			
LIP	−44	−46	44
LCereb	−12	−78	−40
RFusif	50	−54	−20
Nouns vs. verbs			
Rcuneus	14	−80	16
RPCing	10	−40	24
RCaud	22	10	0
Siri et al. (2008)			
Action nouns vs. infinitive verbs			
LIF	−46	16	26
LIF	−48	24	−4
Action nouns vs. inflected verbs			
L IF	−46	16	26
L IF	−48	24	−4
Liljeström et al. (2008)			
Verbs vs. nouns			
LSM	−56	−42	26
LMT	−62	−50	8
LSTPole	−46	18	−22
LSMF	−4	18	42
LPC	−52	6	44
RMT	60	−48	12
RIT	54	−66	−4
RCereb	36	−58	−42
RIns	46	8	−8
RAST	50	−2	−14
Nouns (action pictures) vs. verbs			
LIP	−50	−38	38
	−50	−54	48
LSP	−30	−66	52
LPrec	−12	−66	44
RMF	42	34	30
	48	20	42
RSP	34	−64	56
RIP	46	−48	54
Berlingeri et al. (2008)			
Verbs vs. nouns			
LIF	−36	22	2
LIns	−32	20	2
LParacentral	−10	−38	72
LPrecuneus	−12	−46	74
	−10	−50	66
LMT	−58	−50	6
LSO	−20	−80	28
LMO	−50	−72	6
LCalc	−10	−100	−12
LLing	−12	−82	−6
	−6	−70	6
LCereb	−34	−36	−32
	−46	−54	−26
LPut	−28	14	−2
LHipp	−14	−2	−14

Table 2 (*Continued*)

RParacentral	8	-36	66
RSP	26	−56	60
RPrecuneus	10	−42	60
RMT	52	−76	8
	52	−66	0
RIT	48	−34	−20
RSO	24	−90	34
	22	−94	26
RMO	38	−86	6
RCalc	16	−90	4
	12	−92	12
RCereb	44	−44	−28
	22	−74	−16
4. Valence judgment			
Longe et al. (2007)			
Verb stems vs. noun stems	–		
Inflected verbs vs. inflected nouns			
LIF	−40	8	12
LMT	−51	−42	9
Tyler et al. (2008)			
Verb phrases vs. noun phrases			
LMT	−52	−58	6
Noun phrases vs. verb phrases	–		
5. Lexical decision			
Perani et al. (1999)			
Verbs vs. nouns			
LMF	−28	28	28
LIF	−36	30	20
LSP	−8	−42	80
LST	−48	6	−8
LMT	−48	−48	4
LIO	−42	−90	−20
LLing	−22	−70	4
RLent	26	−8	8
Nouns vs. verbs	–		
Fujimaki et al. (1999)			
no difference			
Tyler et al. (2001)			
Exp 1: verbs vs. nouns			
RSubNigra	12	−22	−6
Nouns vs. verbs	–		
Li et al. (2004)			
Nouns vs. verbs			
RCaud			
Verbs vs. nouns	–		
Yokoyama et al. (2006)			
Active verb vs. noun	–		
Passive verb vs. active verb			
LIF	−42	38	−4
LPMF	−48	4	44
Passive verb vs. noun			
LLing	−10	−94	−2
LMT	−58	−38	4
LPMF	−52	−2	40
6. Passive listening			
Vigliocco et al. (2006)			
No difference			
7. Morphological tasks			
Shapiro et al. (2005)			
Verbs vs. nouns			
LIF	−24	23	−5
LSF	−16	48	20
LST	−32	14	−28
LIns	−40	−34	20
RCereb	16	−83	−29
Nouns vs. verbs			
LLing	−8	89	−2
LFusif	−28	−36	−15
LThal	−16	−11	12
RCereb	24	−59	−17
RPostC	48	−18	27
RIns	36	16	7
RST	63	−4	0

Table 2 (*Continued*)

RST	67	−27	12
Shapiro et al. (2006)			
Verbs vs. nouns			
LMF	−46	6	40
LSP	−32	−57	64
LST	−57	−40	9
RIP	38	−48	−48
Nouns vs. verbs			
LSF	−22	59	23
LFusif\	−36	−42	−16
RParahipp	24	−17	−19
Palti et al. (2007)			
Verb vs. nouns			
LIF	−47	7	14 sem task only
LPMF	−25	9	51 morph task only
LSTS	−54	−36	3 both
Berlingeri et al. (2008)			
Nouns vs. verbs			
LIF, pars triang	−52	24	2
	−38	36	18
LIF, pars orb	−44	28	− 14
LIPlob	−46	−46	62
LPrecuneus	−8	−72	62
LMO	−24	−88	16
LSO	−18	−80	42
LCereb	−38	−72	−28
RCereb	36	−74	−30
Verbs vs. nouns			
LSF	−12	12	54
LPrecentral	−26	−18	62
	−32	−24	58
LSMA	−6	−12	64
LMCing	−4	−38	46
	−2	−40	50
RPrecentral	18	−30	66
	16	−26	64
RSMA	4	−20	58
	12	−8	54
RMCing	2	−34	52
RPostcentral	16	−34	64
	20	−40	64
RParacentral	6	−32	56
RPrecuneus	4	−38	56
	2	−42	56
RParahipp	16	−2	−16
RPallidum	22	−4	4
Burton et al. (2008)			
Verbs vs. nouns			
L MTG	−53	−66	17
L STG	−36	14	−24

L, R = Left, Right; I,M,S,A,Post = Inferior, Middle, Superior, Anterior, Posterior; F,P,T,O = Frontal, Parietal, Temporal, Occipital; SMA = supplementary motor area; Cing = cingulus; Sulc = sulcus; Junc = junction; Cereb = cerebellum; Orb = orbital; Fusif = fusifrom; Ang = angular; Thal = thalamus; Put, Pall = putamen, pallidum; Caud = caudate; Ling = lingual; Hipp, Parahipp = hippocampal, parahippocampal.

The situation is different in studies that used tasks that engage semantic processing to a lesser extent, such as lexical decision or listening to words, and carried out in different languages. In a study using passive listening in English, in which semantics was controlled by using only words (nouns and verbs) referring to events, no greater activations for nouns or verbs were reported (Vigliocco et al., 2006). Reliable left inferior frontal activations for the verb–noun contrast were reported in lexical decision studies by Perani et al. (1999), in Italian, and by Yokoyama et al. (2006) on passive Japanese verbs and in studies in which the task overtly engaged morphosyntactic processes (Shapiro et al., 2005; Palti et al., 2007). In the studies by Shapiro et al. (2006) noun-specific activations in the left fusiform are also reported in addition to verb-specific activations in left middle frontal gyrus.

Let us take a closer look at those studies that have lessened or eliminated the confound with semantics. The results of these studies seem to be mixed at a first glance; however, they provide a relatively clear-cut picture, once task and language-related demands are taken into account. As we have already discussed, because verbs are more complex than nouns at a variety of levels, greater activations for verbs may come about whenever the task used in the study engages processes beyond simple lexical retrieval. Moreover, there are differences in the manner and degree of regularity in which languages mark nouns and verbs at the syntactic and morpho-phonological level, interacting with experimental task demands. Greater activations for verbs than nouns in left IFG were reported in studies that used tasks that required an explicit decision such as lexical decision (Perani et al., 1999) or semantic decision (Tyler et al., 2004), reflecting morphosyntactic processes that may be more demanding for verbs than nouns, as well as the greater processing demands imposed by verbs than nouns (see Binder et al., 2004; Thompson-Schill et al., 1997; Vigliocco et al., 2006). This possibility has been directly addressed in a study by Longe et al. (2007). Greater activations of left IFG for verbs than nouns were observed when English speakers made semantic judgements on inflected words but not when they made judgments on the same words presented in an uninflected form.

In an different attempt to control for the semantic correlates of noun–verb differences, in a fMRI study, Shapiro and colleagues (2006) considered only areas of significant activations emerging both when speakers were carrying out the morphological transformation task, described earlier, with real words and pseudowords. Significantly greater activations for nouns across experiments were observed within the left fusiform gyrus (BA 20). Significant greater activations for verbs were found in left prefrontal cortex (BA 9) and in left superior parietal cortex (BA 7), leading to the hypothesis (depicted in Figure 2) that morpho-syntactic processes that apply to nouns and to verbs engage partly separable neural networks. However, as we have already discussed, these stimuli still conflate semantics and grammatical class; a semantic account of these results is supported by the specific networks that showed greater activation for nouns (fusiform gyrus) and verbs (fronto-parietal action network).

Bedny et al. (2008) attempted to separate the contribution of a specific aspect of semantic reference (biological motion) and grammatical class. The subjects had to perform a relatedness judgement task of word pairs, which included verbs and nouns with three classes of reference (high motion: action verbs and animals; intermediate motion: change of status/bodily function and tools; low motion: mental and inanimate non tools). The areas associated with motion perception were independently localised with a biological motion task. One of several results of the experiment is that action verbs resulted in higher left posterior temporal activation than animal names. While the stimuli were matched for motion content, it is clear that they were not matched for specific action content, as human action probably included manipulation, which is clearly not relevant for animal names.

A different approach to controlling for the semantic correlates of grammatical class as well as the task demands was used in a PET study by Vigliocco et al. (2006) in Italian. In this study (as in the ERP study by Barber et al., in press), we used only words referring to events, either nouns (e.g., *corsa* [run]) or verbs (e.g., *galoppa* [(s/he) gallops]), and either referring to sensation (e.g., *solletico* [tickle]) or motion (e.g., *giravolta* [twirl]). Participants were presented auditorily with blocks of sensory or motor nouns or verbs and asked to simply listen to the words. Thus, the task did not directly engage decision processes, nor processes of morphosyntactic integration. Whereas significant activations related to differences between sensory and motion words were found in anterior temporal cortex (for sensory words), and in primary motor cortex (for motion

Picture	Infinitive Verb	Inflected Verb	Action Noun
	**Ballare** [to dance]	**Ballano** [(they) dance]	**Ballo** [the dance]
	**Leggere** [to read]	**Legge** [(she) reads]	**Lettura** [the readng]
	**Saltare** [to jump]	**Salta** [(he) jumps]	**Salto** [the jump]

Fig. 6. Examples of items used in the Siri et al. (2008) picture naming study. The same picture could be named using an infinitive verb, an inflected verb, or an action noun depending upon the experimental block.

words) no specific activations for nouns or verbs were observed. Thus, whereas comprehending words referring to distinct semantic classes (sensation vs. motion) clearly engaged partially distinct neural networks reflecting the selective involvement of multisensory and motor information, comprehending nouns and verbs engaged a common neural system (see also Saccuman et al., 2006). However, it may be argued that the lack of explicit engagement of noun or verb information is responsible for the lack of grammatical class differences in Vigliocco et al.'s study.

In another study on Italian using fMRI, Siri et al. (2008) assessed whether, once semantic factors are controlled, greater activations for verbs than nouns (found in previous studies) could be attributed to the engagement of integration processes, regardless of grammatical class (Siri et al., 2008). Using a mini-block design, they asked native Italian speakers to name the same picture of an event as a verb in citation form, as an inflected verb and as a noun (Fig. 6).

By using the same picture in the different naming conditions the authors eliminated the semantic confound because participants named the same event using either a noun or a verb. Moreover, as the same picture was always presented, any difference could not be attributed to visual processing demands. Importantly, the task, picture naming, fully engaged the language production system from conceptual retrieval to word retrieval, thus, if there were any differences in processing nouns and verbs these should have emerged, taking in account that noun–verb dissociations in the neuropsychological literature have been established using picture naming. A further remark is that producing the infinitive form of a verb (e.g., *ballare* [to dance]) engages lexical retrieval processes, whereas producing the inflected form (e.g., *ballano* [(they) dance]) engages syntactic and morphophonological integration processes in addition to lexical retrieval. This is especially true because Italian is a *pro-drop* language in which the subject of a sentence does not need to be produced (in contrast to English where the subject is obligatory in these kinds of utterances). Therefore, if activations in left IFG were due to engagement of morpho-syntactic integration processes, these activations should be greater in the Inflected Verb than in the Infinitive Verb condition. Finally, if nouns and verbs are processed by the same neural network, and its degree of engagement depends upon processing demands, we expect to observe activations in left IFG to be greater in the noun condition (e.g., *ballo* [the dance]) than in the verb conditions. This is because the nouns we consider here are generally morphologically complex, being derived from the verbs. Importantly, by explicitly instructing participants to name the picture using a noun or a verb, we further ensure the relevance of grammatical class information for the task (in contrast to previous studies that used tasks such as lexical decision in which grammatical class was neither engaged nor relevant to the task, e.g., Perani et al., 1999; Tyler et al., 2001; Vigliocco et al., 2006).

In contrast to previous studies (Perani et al., 1999; Tyler et al., 2004), Siri et al. did not observe any verb-specific activations. They found, instead, noun-specific activations in left IFG, specifically in BA 44 and more ventrally in BA 45/47. Importantly, these noun-specific activations fall in close proximity to the verb-specific activations reported in the aforementioned studies (see Fig. 7). In a follow-up analysis, they showed that the signal change in left IFG was modulated by differences in the processing demands across the three conditions: strongest activation was found for the Action Nouns, intermediate for Inflected Verbs and weakest for Infinitive Verbs. This finding clearly indicates that left IFG engagement is not selectively linked to verb processing. Rather, left IFG is engaged in the processes required for producing an inflected form of a verb (which, as we described in the introduction, can be considered as syntactic and morphological processes) and, to a greater extent, in the processes engaged in producing derived word forms. Thus, not only did they confirm previous findings of a common system underlying noun and verb processing, but also demonstrated that greater activation for verbs in areas within left IFG do not reflect processes specific to verbs, but integration processes modulated by processing demands.

Thus, to summarise, once semantic correlates are controlled, no or limited differences between processing nouns and verbs emerge (either in production or comprehension), unless the task requires the engagement of decision and integration processes. The crucial dimensions, which can thus largely account for the apparently inconsistent results of imaging studies, are semantic confounding, the nature of the task and how this may interact with language-specific processes. In general, single word processing tasks in which the verb and noun stimuli are not matched for semantic content are prone to show verb-related differences which often involve action and motion related areas in the left hemisphere (premotor and motor areas, middle temporal gyrus). The effect may be amplified if the task directly engages semantic processing (semantic judgment, picture naming). The object-related differences are less consistent, possibly reflecting the larger heterogeneity of the semantic reference of (object) noun stimuli.

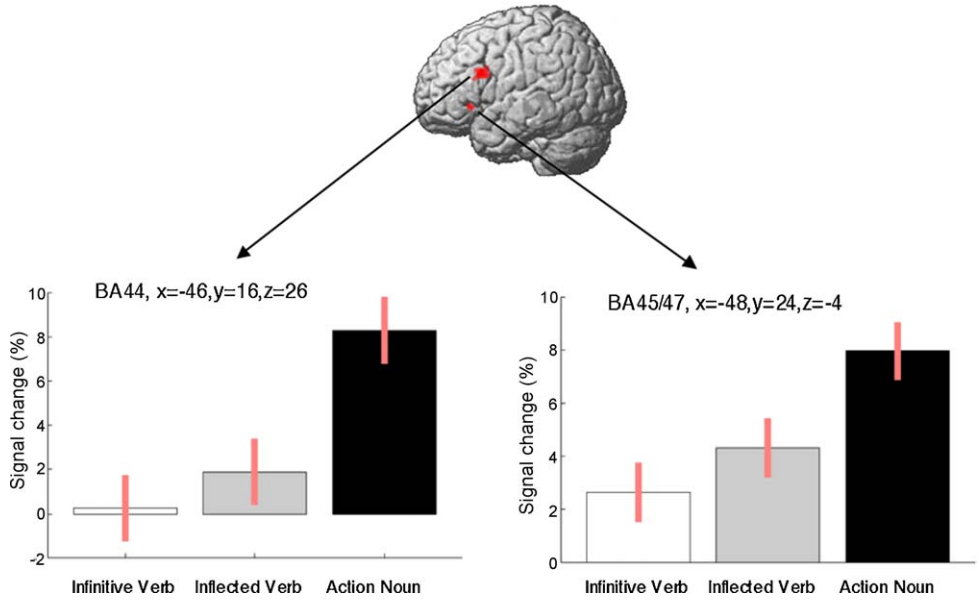

Fig. 7. Results from Siri et al. (2008). Percent signal change for the two peaks of activation within LIFG for Infinitive Verb, Inflected Verb and Action Noun conditions.

7. Overall summary

We have reviewed behavioural, electrophysiological, neuropsychological and imaging work that has addressed the question of whether words belonging to different grammatical classes are represented in segregated neural networks. Once semantic differences between nouns and verbs are taken into account, we observe that behaviourally, grammatical class has a role only when integration processes are highly engaged: when producing sentences in morphologically rich languages but not otherwise. Clear ERP signatures related to grammatical class come about only when speakers are asked to understand words in context and not when the same words are presented in isolation. Lesion data converge in showing the role of semantics and differences in processing demands between nouns and verbs in the interpretation of the double dissociation observed between noun and verb naming. Neuropsychological studies in patients with focal lesions and with neurodegenerative disorders further highlight the role of integration and executive processes in tasks involving verbs. Lesion, TMS and imaging studies clearly converge in indicating the importance of left inferior temporal cortices in object naming and in representing object knowledge, and of prefrontal cortex in action naming and action knowledge, thus supporting hypotheses of neural separation of semantic knowledge (e.g., Martin and Chao, 2001; Martin, 2007; Cappa, 2008). Imaging studies also converge with lesion studies in indicating a role for integration processes, engaging primarily left IFG and middle frontal gyrus, but provide no evidence for neural segregation of nouns and verbs as lexical categories. Below we discuss the implications of the results we have reviewed for the cognitive and neuroanatomical theories of language processing we have outlined at the beginning of the paper.

With regards to psycholinguistic models, the review provides clear evidence against lexicalist theories, especially strong views according to which grammatical class information is automatically and necessarily retrieved when words are retrieved regardless of whether words are used in isolation or in sentential context (e.g., Pickering and Branigan, 1998). Importantly, the lack of strong evidence in favour of neural separability of integration processes that apply to nouns and those that apply to verbs, leads us to favour cognitive views in which words from different grammatical class do not use specialised neural or cognitive systems, thus, models in which both noun and verb processing are carried out by a shared combinatorial procedural system, or in which the noun–verb distinction emerges as a consequence of different constraints.

With regards to neuroanatomical models, the data we have reported here are most compatible with views in which a shared neural network underlies the processing of words from different grammatical categories. Considering imaging studies, with one exception (Shapiro et al., 2006, and here again remains the issue of a plausible semantic interpretation) the evidence clearly indicates that a common neural system comprising the left IFG (not limited to Broca's region) is engaged in the morphosyntactic processing of nouns and verbs. This system is more highly engaged in verb morphosyntactic processing than in noun morphosyntactic processing because of verb processing imposes grater demands than noun processing in most cases, but this pattern can be reversed if experiments use nouns that demand more processing resources than verbs (as in the study by Siri et al., 2008).

Whereas the evidence reviewed here strongly suggests that there are no distinct brain signatures for processing words from different grammatical class, it also provides strong support for the existence of a neural segregation of semantic knowledge (e.g., Martin and Chao, 2001; Martin, 2007; Cappa, 2008). Accessing the semantic content of words is associated with the activation of brain areas, which are related to the specific semantic information conveyed by the words in broad agreement with embodiment theories of cognition (e.g., Barsalou et al., 2003). With the exception of emergentist views, grounded in cognitive linguistic approaches, the psycholinguistic models we have discussed view these powerful semantic constraints as independent from grammatical class. The lack of any clear signature of grammatical class when these semantic correlations are controlled, however, is problematic for such views. We conclude the paper below presenting a version of emergentist views constrained by insight from typological theories of grammatical class, namely, theories aiming at capturing general principles behind the extensive degree of variability across the world's languages.

8. General conclusions: A typological emergentist view of grammatical class in the brain

Our review has shown important constraints for theoretical proposals that aim to provide a neuroanatomical understanding of how words belonging to different grammatical classes are processed. In addition, it has highlighted the important role for cross-linguistic variability in understanding the results of different studies. Cross-linguistic differences in how grammatical class is expressed have been largely neglected in psycholinguistic and neural theories of grammatical class processing (for exceptions see MacWhinney et al., 1984; Iwasaki et al., 2008; Tyler et al., 2004; Vigliocco et al., 2006) . Nonetheless, taking into account possible interactions between cross-linguistic differences and differences in task demands, may provide a key to accounting for otherwise conflicting results. In this light, particularly interesting is to consider the findings we have reviewed in light of *typological theories of grammatical class*.

The two overarching findings emerging from the review, namely, the clear neural separability between the processing of object and action words, and the fact that grammatical class effects emerge or become stronger for tasks and languages imposing greater processing demands are consistent with the two general principles described by typological linguistics as underlying grammatical class membership across languages. Croft (2000) proposes that pragmatic function (whether a given word refers to or predicates about entities) and semantic membership (object or action) jointly provide the first and foundational principle for building prototypical noun and verb classes. Considering the evidence reviewed, it is clearly the case that whenever the studies used prototypical nouns and verbs (thus as we have put it, confounding these important pragmatic/semantic dimensions with grammatical class) there are clear behavioural effects and neural differences. The lexicalist and combinatorial views presented in the introduction recognise the importance of these pragmatic/semantic factors but nonetheless postulate that grammatical class is independent of them. This assumption of independence is reflected in the neural models that assume that words from different grammatical class engage partially distinct representations or processes. This is not the case for emergentist views for which, instead the pragmatic/semantic factors drive the segregation of words belonging to different grammatical classes, in line with the typological claims above. These pragmatic/semantic forces would be foundational in the learning of grammatical class. Developmentally, children would begin by learning words referring to prototypical objects and prototypical actions, and associating these with different linguistic contexts (e.g., words referring to objects are often preceded by the word "the"), thus developing the distinction between nouns and verbs. When they begin to learn abstract words, this already established distinction (based on semantically prototypical objects vs. actions) would be extended to the less prototypical cases.

Thus, pragmatic/semantic forces provide a universal first principle for grammatical class distinctions. These are insufficient, however, to correctly classify all members of noun or verb classes across languages. Typological theory suggests a second cross-linguistically valid principle for the classification of words into grammatical classes, related to probabilistic distributional cues in sentences. All languages have cues related to nouns' and verbs' syntactic behaviour in sentences (e.g., position in sentences, type of particles associated with them, etc.) and related to their morpho-syntactic marking (e.g., types of inflections on nouns vs. verbs). Moreover, Croft (2000) observed that across languages, prototypical members can exhibit more flexible syntactic behaviours while non-prototypical members can exhibit more flexible morpho-syntactic behaviours. We will refer to syntactic behaviour and morpho-syntactic marking jointly as distributional cues.

In the emergentist view, these distributional cues would combine with pragmatic/semantic cues (and also with phonological cues to grammatical class) to determine the difficulty of classifying a specific word into one or the other class, and hence how demanding it is to learn and process it. The pragmatic/semantic cues play the most important role: prototypical members are easier to learn and to use. Non-prototypical members, which do not benefit from pragmatic/semantic factors, would be harder to learn and more difficult to process, because distributional cues are more subtle and not as reliable. Throughout our review, we have seen repeatedly that it is when the processing demands increase that we see effects of grammatical class. We have seen that for non-prototypical members (action nouns), behavioural effects may be present (in Italian, Vigliocco et al., 2005) or absent (in Japanese, Iwasaki et al., 2008) depending upon the weight of distributional information (greater in Italian than in Japanese). EEG studies show that words that are ambiguous with respect to grammatical class behave differently than unambiguous words (Federmeier et al., 2000). It can be argued that the reliability of distributional information is greater for unambiguous than for ambiguous words. Left IFG is more strongly engaged in the processing of verbs than nouns in English, when the task requires greater attention toward morphological markers (Tyler et al., 2004) and in Italian when subjects are producing inflected verbs (Siri et al., 2008). Crucially, however, in Italian, action nouns engage left IFG to an even greater extent than verbs, as one would expect, given that for action nouns so many cues point in the wrong direction.

In terms of neural systems, the basic assumption is that the processing of words from different grammatical classes will engage partially separable networks: fronto-parietal, related to action knowledge; inferotemporal, related to object knowledge (both underscoring the pragmatic/semantic foundation) and left prefrontal, in particular including IFG, related to the reliability of distributional information. Empirical questions for future research include whether manipulations of the reliability of distributional information within or between languages lead to similar or different changes in left IFG; the extent to which these activations are linked to working memory; and the extent to which different types of distributional cues all involve the same overlapping network or, instead, show some degree of separability. This latter in particular will allow us to more fully test emergentist views in which prefrontal cortex underscores integration of all the different cues (e.g., Bates and MacWhinney, 1989; Elman, 2004).

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