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Distinguishable neural correlates of verbs and nouns: A MEG study on homonyms

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ABSTRACT

The dissociability of nouns and verbs and of their morphosyntactic operations has been firmly established by lesion data. However, the hypothesis that they are processed by distinct neural substrates is inconsistently supported by neuroimaging studies. We tackled this issue in a silent reading experiment during MEG. Participants silently read noun/verb homonyms in minimal syntactic context: article-noun (NPs), pronoun-verb (VPs) (e.g., *il ballo/i balli*, the dance/the dances; *io ballo/tu balli*, I dance/you dance). Homonyms allow to rule out prelexical or postlexical nuisance factors—they are orthographically and phonologically identical, but serve different grammatical functions depending on context. Under these experimental conditions, different activity to nouns and verbs can be confidently attributed to representational/processing distinctions. At the sensor level, three components of event-related magnetic fields were observed for the function word and four for the content word, but Global Field Power (GFP) analysis only showed differences between VPs and NPs at several but very short time windows. By contrast, source level analysis based on Minimum Norm Estimates (MNE) yielded significantly greater activity for VPs in left frontal areas and in a left frontoparietal network at late time windows (380–397 and 393–409 ms). These results are fully consistent with lesion data, and show that verbs and nouns are processed differently in the brain. Frontal and parietal activation to verbs might correspond to morphosyntactic processes and to working memory recruitment (or thematic role assignment), respectively. Findings are consistent with the view that nouns and verbs and their morphosyntactic operations involve at least partially distinct neural substrates. However, they do not entirely rule out that nouns and verbs are processed in a shared neural substrate, and that differences result from greater complexity of verbal morphosyntax.

1. Introduction

The dissociability between the processing of nouns and verbs has been extensively documented in aphasiological data, and in a variety of tasks (Caramazza & Hillis, 1991; Damasio & Tranel, 1993; Miceli, Silveri, Villa, & Caramazza, 1984; Shapiro & Caramazza, 2003; Tsapkini, Jarema, & Kehayia, 2002). The most robust anatomical findings associate impaired verb and noun processing with damage to left frontal and left temporal regions, respectively (e.g. Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001; Damasio & Tranel, 1993; Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994).

Even though the functional dissociability and its most typical neural correlates have been repeatedly demonstrated in brain-damaged patients, the search for its neural underpinnings via neuroimaging techniques has yielded inconsistent results. Some PET studies showed left prefrontal and middle frontal cortices to be selectively activated by verbs (Petersen, Fox, Posner, Mintum, & Raichle, 1989; Raichle et al., 1994; Wise et al., 1991). However, other PET studies failed to identify differential neuronal substrates for nouns and verbs (e.g. Tyler, Russell, Fadili, & Moss, 2001; Warburton et al., 1996), even though in some cases greater activation to verbs than nouns was observed (Perani et al., 1999). A large variability exists also in the fMRI literature. While some investigations show greater activation for verbs in the left inferior prefrontal cortex (e.g. Davis, Meunier, & Marslen-Wilson, 2004; Finocchiaro, Basso, Giovenzana, & Caramazza, 2010; Shapiro, Moo, & Caramazza, 2006; Yokoyama et al., 2006), others report on contrasting results. Thus, while in some cases verb processing was

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linked to left middle temporal gyrus activation (Longe, Randall, Stamatakis, & Tyler, 2007; Tyler, Randall, & Stamatakis, 2008; Bedny, Caramazza, Grossman, Pascual-Leone, & Saxe, 2008), in others it highlighted a very extensive neural network (Berlingeri et al., 2008), or the same circumscribed brain regions as nouns (Siri et al., 2008). In the abovementioned studies, activation in response to nouns was either unidentifiable (Longe et al., 2007; Tyler et al., 2008) or less robust than to verbs (Berlingeri et al., 2008; Siri et al., 2008). And, in a recent study, noun phrases activated left inferior prefrontal regions more than verbs (Pulvermüller, Cook, & Hauk, 2012). Contrasting results prompted the proposal that the networks underlying noun and verb processing are not spatially segregated (e.g. Crepaldi, Berlingeri, Paulesu, & Luzzatti, 2011; Vigliocco, Vinson, Druks, Barber, & Cappa, 2011).

Repetitive Transcranial Magnetic Stimulation (rTMS) and event related potential (ERP) studies also documented distinctions between grammatical categories, but diverged when identifying the neural underpinnings of verb processing. While in a study stimulation of the left prefrontal cortex disrupted verb production (Shapiro, Pascual-Leone, Mottaghy, Gangitano, & Caramazza, 2001), another study failed to confirm this finding (Cappa, Sandrini, Rossini, Sosta, & Miniussi, 2002); and yet another identified the anterior portion of the left middle frontal gyrus as the critical area for inflected verb production (Cappelletti, Fregni, Shapiro, Pascual-Leone, & Caramazza, 2008). ERP studies repeatedly showed increased left-lateralized anterior positivity associated with the processing of verbs as compared to nouns (Dehaene, 1995; Federmeier, Segal, Lombrozo, & Kutas, 2000). However, while different temporal patterns of activation for nouns and verbs are a consistent finding in the ERP literature, topographical differences between the two grammatical categories are variable (Gomes, Ritter, Tartter, Vaughan, & Rosen, 1997; Khader & Rösler, 2004; Pulvermüller, Preißl, Lutzenberger, & Birbaumer, 1996; Pulvermüller, Preißl, & Lutzenberger, 1999). In another study, ERP activity was affected both by grammatical class and by semantic properties (Barber, Kousta, Otten, & Vigliocco, 2010).

We used magnetoencephalography (MEG), that offers a potentially more promising approach to the problem under investigation than either fMRI/PET, which rely on slow metabolic changes and therefore have limited temporal resolution, or ERP, whose topographical information is rather underspecified and therefore allows limited claims in terms of separation and localization of underlying generators. MEG combines excellent temporal resolution with good localization accuracy, at least for superficial cortical sources (Papadelis, Poghosyan, Fenwick, & Ioannides, 2009). Therefore, it allows to adequately tackle our primary questions—establishing if nouns and verbs activate identical or distinct neural substrates, and if they do so to the same extent and at the same or different points in time.

Available MEG findings on noun/verb processing are controversial. In picture naming studies, Sörös, Cornelissen, Laine, and Salmelin (2003) found identical patterns of activation for both word types, but Liljeström, Hultén, Parkkonen, and Salmelin (2009) observed differences only at an early time window (100–200 ms). In this latter study, activation of right frontal and bilateral parietal cortex was enhanced by nouns; the anterior-superior temporal lobe was activated by verbs, but weakly and irregularly across subjects. Observations from silent reading are also inconsistent. In Xiang and Xiao (2009), the same regions were activated by nouns and verbs at an early stage, and spatiotemporal sequences diverged at late latencies. In a category judgment task, Fiebach, Maess, and Friederici (2002) examined the effects of syntactic context. When nouns and verbs were presented in isolation, no differences were found in the left hemisphere. However, when they were presented in a minimal syntactic context, nouns elicited stronger magnetic fields over left posterior temporal regions.

Inconsistent MEG results might be due to different causes. Picture naming paradigms are problematic, as noun and verb stimuli typically differ in visual complexity and require different processes for response elicitation (nouns are on average more referential, concrete and imageable). For example, a picture of scissors suffices to precipitate naming of the object, but in order to elicit "to cut", both scissors and something being cut must be shown. In addition, naming a target verb requires more than analyzing the physical features of the stimulus—saying "to fall" in response to a picture requires not only accurate visuoperceptual analysis, but also assumptions on events that take place before and after the instant captured in the stimulus. These nuisance factors may elicit different activations, independent of grammatical class distinctions. At face value, silent reading tasks are less problematic, as written nouns and verbs can be matched for psycholinguistic variables (length, frequency of usage, etc.). However, also silent reading of unambiguous nouns and verbs (Xiang & Xiao, 2009; Fiebach et al., 2002) is not problem-free, as selected stimuli visually and orthographically different, and the corresponding covert responses may activate different phonological word forms. Given the sensitivity of MEG to even minor changes in visual stimulus features (e.g., Ramkumar, Jas, Pannasch, Hari, & Parkkonen, 2013), also in this case nuisance factors may interfere with results, and render their interpretation problematic.

To overcome these shortcomings, we presented homonyms in a silent reading paradigm, to native speakers of Italian. Homonyms were selected because they are orthographically and phonologically identical[1], even though they serve different grammatical functions, depending on syntactic context. This choice ensures that during the experimental procedure visuo-perceptual, orthographic, phonological and subvocal processes are engaged to exactly the same extent by nouns and verbs, thus eliminating critical nuisance factors. Under these experimental conditions, different MEG responses to NPs and VPs can be legitimately ascribed to genuine representational/processing (and neural) distinctions between nouns and verbs. An additional advantage afforded by Italian homonyms is that for the most part they are strictly related semantically (e.g., *ballo*, the dance/I dance; *canti*, the songs/you sing; *cena*, the dinner/he has dinner). Therefore, results allow to address a debated issue—whether putative differences between nouns and verbs are the result of distinctions at the lexical–grammatical or at the semantic level (for contrasting views, see Shapiro & Caramazza, 2003; Vigliocco et al., 2011).

Neuromagnetic brain responses were analyzed by using the Minimum-Norm Estimates (MNE) (Hämäläinen & Ilmoniemi, 1984, 1994; Hauk, 2004). Results help identify the neural underpinnings of NP and VP processing, and allow discussing some mechanisms potentially underlying noun/verb dissociations.

2. Materials and methods

2.1. Participants

Thirteen healthy native Italian speakers participated in this study. They were all right-handed, with normal or corrected-to-normal vision. None reported a history of significant head injury or neurological disease. Prior to testing, written informed consent was obtained from each participant. Compensation was given for participation, following completion of the experiment. The research protocol was approved by the local ethical committee and the study complied with the Declaration of Helsinki. MEG recordings of 12 participants (age: 23–34, mean age: 27; five female and seven male) entered the analysis of the present study. Data from a participant were excluded due to heavy artifact contamination.

[1] Owing to the transparency of the relationships between orthography and pronunciation in Italian, words that are homographs are also homophones, with an extremely limited number of exceptions.