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A brain electrical signature of left-lateralized semantic activation from single words ☆

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ABSTRACT

Lesion and imaging studies consistently indicate a left-lateralization of semantic language processing in human temporo-parietal cortex. Surprisingly, electrocortical measures, which allow a direct assessment of brain activity and the tracking of cognitive functions with millisecond precision, have not yet been used to capture this hemispheric lateralization, at least with respect to posterior portions of this effect. Using event-related potentials, we employed a simple single-word reading paradigm to compare neural activity during three tasks requiring different degrees of semantic processing. As expected, we were able to derive a simple temporo-parietal left-right asymmetry index peaking around 300 ms into word processing that neatly tracks the degree of semantic activation. The validity of this measure in specifically capturing verbal semantic activation was further supported by a significant relation to verbal intelligence. We thus posit that it represents a promising tool to monitor verbal semantic processing in the brain with little technological effort and in a minimal experimental setup.

1. Introduction

A unique and defining characteristic of the human brain is the elaborate system that affords us our highly developed linguistic capabilities. One of the most essential functions of language is the representation of semantics, which is in its simplest form the access to linguistic word meaning, but can also comprise the activation of related characteristics, superordinate categories, up to multifaceted networks with associated characteristics as well as related world knowledge (Hagoort, Hald, Bastiaansen, & Petersson, 2004). Since the late nineteenth century, there has been consensus that the representation of semantics relies heavily, albeit not exclusively, on the activity of neurons in the left temporal lobe (Binder & Desai, 2011; Binder, Desai, Graves, & Conant, 2009; DeWitt & Rauschecker, 2013; Friederici, 2012; Hickok & Poeppel, 2007; Price, 2000, 2012; Pulvermüller, Shtyrov, & Hauk, 2009; Rodd, Vitello, Woollams, & Adank, 2015; Turken & Dronkers, 2011; Wang et al., 2015). This notion derives almost exclusively from work on rare lesions and studies employing intricate neuroimaging techniques (Binder & Desai, 2011; Binder et al., 2009; Price, 2000, 2012). Somewhat surprisingly, electroencephalography (EEG), which allows to monitor brain activity directly and with remarkable temporal precision, has rarely been used to capture and contest the assumed lateralization of semantic processing.

Prior electrophysiological assessments of posterior left-lateralized language processing predominantly focused on earlier, low-level stages of word processing (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999) or visual discrimination in the left occipito-temporal cortex (Lochy, Van Belle, & Rossion, 2015). Visual word analysis is reliably indicated by the N1 (or N170) component of the event-related potential (ERP) evoked by any kind of orthographic stimuli, which is largest over left occipito-temporal sites (Bentin et al., 1999; Hauk & Pulvermüller, 2004; Maurer, Brandeis, & McCandliss, 2005; Rabovsky, Sommer, & Abdel Rahman, 2012; Simon, Bernard, Largy, Lalonde, & Rebai, 2004).

With regard to semantics, studies investigating ERPs mostly examined unlateralized processes, as typically indicated by the centro-parietal N400 component (Kutas & Federmeier, 2011; Kutas & Hillyard, 1980). This broad negativity peaks relatively late, approximately 400–450 ms after stimulus onset, and shows a small, yet consistent bias to the right hemisphere, at least for visual presentation (Lau, Phillips, & Poeppel, 2008). It is typically elicited by violations of context-induced expectations, rather than by semantic encoding *per se* (Lau, Holcomb, & Kuperberg, 2013), and was also found with magnetoencephalography (MEG; Halgren et al., 2002; Lau, Almeida, Hines, & Poeppel, 2009). These studies

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converge on a left temporal source of the N400, thus deviating from the central scalp distribution found by most ERP studies. This discrepancy between surface distribution and source lateralization of the N400 might rely on the fact that the negative pole of the electrical dipole responsible for N400 is located in the left hemisphere, yet oriented toward the right hemisphere (Lau et al., 2008). Context or word-class effects related to semantics have also been observed for the early (typically left-lateralized) N1 (Sereno, Brewer, & O'Donnell, 2003; Skrandies, 1998). However, bilateral N1 effects of sentence context (Penolazzi, Hauk, & Pulvermüller, 2007) and even right-lateralized N1 effects of word valence (Kissler, Herbert, Winkler, & Junghöfer, 2009) have also been reported. Using MEG, Pulvermüller, Assadollahi, and Elbert (2001) found left-lateralized semantic effects on N1 amplitude. Furthermore, early congruency effects for words in a sentence context were found at left superior temporal and left medial temporal regions in the time window of the word-related N1 (179–204 ms) using event-related optical signals (EROS; Tse et al., 2007). Moreover, ERP effects of semantic category membership, semantic richness, and emotional content were observed at around 200 ms, thus occurring prior to the N400, but after the initial N1. However, interactions of these effects with hemisphere were not reported in some studies (Moscoso del Prado Martín, Hauk, & Pulvermüller, 2006; Rabovsky et al., 2012), whereas a left-lateralization was revealed in other studies in which words of different categories had to be discriminated (Dehaene, 1995; Hauk & Pulvermüller, 2004: for face-related action words).

Altogether, there is evidence of early semantic influences from EEG and MEG, but temporo-parietal, left-lateralized correlates of semantic activation *per se*, as suggested by neuroimaging studies, are still pending, with one recent exception: Gibbons, Bachmann, and Stahl (2014) reported that deeper processing of affective words in some participants as opposed to others, was accompanied by a left-side reduction of centro-parietal and parietal P3 (288–380 ms). This effect was interpreted as a left-side ERP processing negativity, which overlaps the P3 and indicates semantic processing. However, this conclusion was largely post-hoc, as depth of processing was not experimentally manipulated, and it cannot be excluded that this type of finding is restricted to affective words.

The aim of the present study was to replicate the finding of a left-posterior ERP negativity indicating semantic activation from single words (Gibbons et al., 2014), but with the use of an experimental manipulation of depth of semantic processing and with non-affective word stimuli. Such a finding would complement neuroimaging findings of left-lateralized semantic activation in temporo-parietal brain regions. Ultimately, we aimed at introducing a straightforward left-right asymmetry index of semantic activation in the ERP, making use of its particularly high temporal resolution and low costs.

To this end, based on a principle often employed in neuroimaging (Abbott, Waites, Lillywhite, & Jackson, 2010; Seghier, 2008; Wilke & Lidzba, 2007), we subtracted right-side from left-side word-induced activity, suppressing all activity that is common to both hemispheres and carving out neural activation that is specific to one side. We thus followed the basic approach of *difference waves*, which are generally assumed to allow us to track the time course and spatial distribution of an underlying ERP component particularly precisely (Luck, 2014). In view of the assumption of a left-hemispheric semantic (relative) processing negativity superimposed on the unlateralized P3 (Gibbons et al., 2014), it seemed promising to assess how tasks requiring different degrees of semantic activation would affect left-right difference waves in in a within-subject design. Unlike in the study by Gibbons et al. (2014), which was based on a between-subjects comparison of ERPs in one and the same task, we were able to compute within-subject ERP differences between tasks, to isolate the activity specific to semantic processing. However, tasks may also differ with respect to unlateralized ERP indices of general attentive processing, such as posterior P3. Therefore, to truly isolate differences between tasks in left-lateralized language-related processing in each single participant, a lateralization index is additionally needed, depicting the difference between left- and right-side activity. This then represents a twofold application of the difference-wave approach, which is best suited for the present purposes. Generally, lateralization indices are quite common in EEG research. For example, the lateralized readiness potential (LRP) displays the cortical asymmetry resulting from the preparation of a motor response with one hand (Eimer, 1998) and is defined as the voltage difference between contralateral and ipsilateral electrode sites (Luck et al., 2009) relative to the respective response hand. However, asymmetry indices have not yet been used to track lateralized language processing. Using right-side activation as a conservative baseline, an asymmetry measure suppresses unlateralized processes that may be largely nonspecific to conceptual activation, thus selectively unfolding the expected left-hemispheric preponderance during semantic processing.

Our *first* hypothesis concerned a general left-lateralization of temporo-parietal brain activity in response to the visual word stimuli, in terms of a (relative) left-side ERP negativity at around 300 ms. Moreover, this asymmetry should be more pronounced when words were read during a semantic task than during tasks requiring no activation of the words' concepts, which would support the conclusions of Gibbons et al. (2014). As we assumed the source of this effect in the left hemisphere, we expected stronger task-related ERP differences in the left compared to the right hemisphere. *Secondly*, as a replication hypothesis, we expected a left-lateralized occipito-temporal N1 component in all tasks (Bentin et al., 1999; Maurer et al., 2005). However, as an index of visual attention (Hillyard, Vogel, & Luck, 1998), N1 amplitude should be larger for tasks requiring active engagement with the words, compared to a passive task (see below), but should not yet discriminate between a semantic and a non-semantic active task. Thus, N1 can be seen as a manipulation check, ensuring that participants processed the words less attentively in a passive condition than in the other two conditions.

We tested these hypotheses in a single-word reading paradigm employing three tasks. While EEG was recorded, participants were first instructed to passively watch a series of words (*Form* condition). This constituted a baseline condition mainly involving visual word-form processing. In a second condition, participants had to imagine the articulation of the presented words (*Articulation* condition), and in a third condition, participants mentally counted words representing animals (*Meaning* condition). While the Form condition requires less active processing of the words, the Meaning condition differs from the two others most clearly in terms of semantic processing: The activation of each word's semantic representation is *necessary* in order to correctly classify each word. In the Articulation condition, semantic activation might incidentally occur; however, it is not necessary. Given this fine distinction, the Articulation condition constitutes a very strict control, especially so because some authors even assumed "[w]ord reading and the access to their meaning [...] to be irrepressible" (Simon et al., 2004, p. 1404). Thus, any difference between the Meaning and the Articulation condition provides a conservative estimate of semantic activation.

2. Materials and methods

2.1. Participants

The study protocol was in accordance with the Declaration of Helsinki and was approved by the local ethics committee. Forty