CORTEX 49 (2013) 711–721

Available online at www.sciencedirect.com

SciVerse ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Research report

Left parietal alpha enhancement during working memory-intensive sentence processing

Lars Meyer [a,*], Jonas Obleser [b] and Angela D. Friederici [a]

[a] Department of Neuropsychology, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany
[b] Max Planck Research Group "Auditory Cognition", Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

ARTICLE INFO

Article history:
Received 21 September 2011
Reviewed 16 November 2011
Revised 21 December 2011
Accepted 5 March 2012
Action editor Bradley Postle
Published online 20 March 2012

Keywords:
Alpha oscillations
Argument-verb dependency
Sentence processing
Source localization
Verbal working memory

ABSTRACT

Both functional magnetic resonance imaging (fMRI) and event-related brain potential (ERP) studies have shown that verbal working memory plays an important role during sentence processing. There is growing evidence from outside of sentence processing that human alpha oscillations (7–13 Hz) play a critical role in working memory. This study aims to link this to the sentence processing domain. Time-frequency analyses and source localization were performed on electroencephalography (EEG) data that were recorded during the processing of auditorily presented sentences involving either a short or a long distance between an argument (subject or object) and the respective sentence-final verb. We reasoned that oscillatory activity in the alpha band should increase during sentences with longer argument-verb distances, since decreased temporal proximity should result in increased memory demands. When verbal working memory-intensive long-dependency sentences were compared to short-dependency sentences, a sustained oscillatory enhancement at 10 Hz was found during storage prior to the sentence-final verb, turning into a transient power increase in the beta band (13–20 Hz) at the sentence-final verb. The sources of the alpha oscillations were localized to bilaterally occipital and left parietal cortices. Only the source activity in the left parietal cortex was negatively correlated with verbal working memory abilities. These findings indicate that the parsimonious role of alpha oscillations in domain-general working memory can be extended to language, that is, sentence processing. We suggest that the function of left parietal cortex underlying verbal working memory storage during sentence processing is to inhibit the premature release of verbal information that will subsequently be integrated.

1. Introduction

Traditionally, it had been assumed that the human alpha rhythm (7–13 Hz) represents an idle cortical state (Berger, 1929), based mainly on the observation that alpha oscillations increase as a preface to sleep, during eye closure, or motor relaxation (for a review, see Klimesch et al., 2007). More recently it has been proposed that the idea of alpha oscillations as an idling rhythm of the cortex may not reflect the full picture, in particular in the auditory domain (for a review, see Weisz et al., 2011). Following Lehtelä et al.'s (1997) report of a 10 Hz rhythm in primary auditory cortex which is sensitive to

* *Corresponding author*. Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstraße 1a, 04103 Leipzig, Germany.
E-mail address: lmeyer@cbs.mpg.de (L. Meyer).
0010-9452/$ – see front matter © 2012 Elsevier Ltd. All rights reserved.
doi:10.1016/j.cortex.2012.03.006

changes in auditory input, a number of recent articles have pointed out the significance of alpha oscillations for verbal working memory. For example, a magnetoencephalography (MEG) study by Jensen et al. (2002) used a modified version of Sternberg's (1966) letter-based working memory paradigm, finding increased alpha power over posterior electrodes with increased verbal working memory load. Along these lines, Leiberg et al. (2006) reported increased alpha activity under conditions of increased verbal working memory storage demands. Finally, Van Dijk et al. (2010) reported increased alpha amplitude during storage of task-relevant pitch information. In sum, there is good evidence that enhanced alpha oscillations are a robust neural correlate of verbal working memory.

Given this role of alpha oscillations in item or pitch retention, we hypothesized that also higher-level cognitive processes in the auditory domain that exhibit increased verbal working memory demands—such as sentence processing—will increase alpha activity as well. Verbal working memory is commonly agreed on to play an important role in sentence processing (Just and Carpenter, 1992; Rogalsky and Hickok, 2010; Waters and Caplan, 1996; Wingfield and Butterworth, 1984). Baddeley and Hitch's (1974) initial work found that concurrent memory load decreases reading comprehension performance, inducing that reading comprehension is subserved by a capacity-constrained verbal working memory. More specific work showed that working memory capacity determines the ability to store and retrieve the arguments (both subject and object) until they can be syntactically linked to the main verb of the sentence and the sentence meaning can be inferred (King and Just, 1991)—which is of particular relevance in languages with sentence constructions requiring the verb to be in sentence-final position such as German and Japanese.

While there is support for an involvement of verbal working memory resources during argument-verb dependency processing (i.e., domain-specific functions), this support is hard to map onto the literature on alpha oscillations during verbal working memory storage outside of the sentence processing domain. Previous event-related brain potential (ERP) studies on verbal working memory from the sentence processing domain rather focused on word ordering processes during sentence processing, mostly triggered by research questions derived from theoretical linguistics. Such studies isolated sustained negative ERP effects for object-first as compared to subject-first sentences (Felser et al., 2003; Fiebach et al., 2001, 2002; Kluender and Kutas, 1993; Phillips et al., 2005; Ueno and Kluender, 2003). However, more general work on working memory, in particular on visual working memory, suggests that the retention of order information may be distinct from mere (that is, order-indifferent) storage: Hsieh et al. (2011) had their participants to focus on either the presence or absence of an item or the order of items in a delayed-response paradigm, obtaining enhanced posterior alpha for storage only, independent of the order of items. Given that behavioral work suggests that argument retrieval in the vicinity of verbs is a mechanism common to both subject- and object-first sentences (Nicol and Swinney, 1989), we hypothesize common oscillatory dynamics of argument storage, independent of the relative order of arguments—as opposed to distinct sustained ERP indices which are sensitive to the relative order of arguments.

The current study on sentence processing was designed to investigate verbal working memory storage processes independent of a particular sentence structure: these are required for the processing of any argument-verb dependency, regardless of the argument order. If alpha oscillations during sentence processing are independent from the processing of order information, such a result may help in disentangling verbal working memory and ordering processes during sentence processing.

While ERP findings from the sentence processing domain are hard to link to the underlying neuroanatomy, a number of functional imaging studies provide information about the neural underpinning of verbal working memory during sentence processing. As an example, Novais-Santos et al. (2007) reported left inferior parietal cortex to increase its activation with the retention interval for disambiguating information in ambiguous sentences, that is, verbal working memory load. In addition, Grossman et al. (2002) found an age-related decrease of brain activation related to increased argument-verb distance in the left parietal cortex, alongside sentence processing difficulties in seniors. The notion of left parietal cortex as potential neural substrate of verbal working memory during sentence processing is in line with meta-analyses, imaging studies and clinical work from outside of sentence processing (Awh et al., 1996, 1995; D'Esposito et al., 1999; Jonides et al., 1998; Leff et al., 2009; Owen et al., 2005; Petrides et al., 1993; Smith and Jonides, 1999; Wager and Smith, 2003). However, other studies focusing on verbal working memory during sentence processing reported Brodmann Area (BA) 45 in the left prefrontal cortex to play a role, using paradigms comparing different syntactic dependencies (Fiebach et al., 2005; Makuuchi et al., 2009; Santi and Grodzinsky, 2007, 2010). Hence, the imaging results for verbal working memory during sentence processing and their relation to the ERP literature are unequivocal, and a temporally more fine-grained method may complement the discussion.

Due to the potential role of cortical alpha oscillations in higher-level cognitive tasks such as sentence processing, we investigated cortical oscillations during the processing of sentences that involve greater working memory load without additionally increasing ordering demands. We hypothesized that any argument—regardless of whether it is a subject or an object—is stored in verbal working memory until the verb position at which retrieval of the argument becomes necessary for sentence interpretation. Consequently, we reasoned that oscillatory activity in the alpha band should increase with verbal working memory demands (Leiberg et al., 2006; Van Dijk et al., 2010) regardless of argument order. Testing this assumption will help to bridge the gap between the emerging literature on alpha oscillations in verbal working memory and the supposed role of verbal working memory during argument-verb dependency processing. In a similar vein, we will link changes in oscillatory power during storage-intensive sentence processing to a classical working memory measure from the sentence processing domain, that is, reading span (Daneman and Carpenter, 1980). Finally, we investigate the neural generators of the observed responses using source localization to provide a tentative link to