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Electrophysiological signatures of phonological and semantic maintenance in sentence repetition

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ABSTRACT

Verbal short-term memory comprises resources for phonological rehearsal, which have been characterized anatomically, and for maintenance of semantic information, which are less understood. Sentence repetition tasks tap both processes interactively. To distinguish brain activity involved in phonological vs. semantic maintenance, we recorded magnetoencephalography during a sentence repetition task, incorporating three manipulations emphasizing one mechanism over the other. Participants heard sentences or word lists and attempted to repeat them verbatim after a 5-second delay. After MEG, participants completed a cued recall task testing how much they remembered of each sentence. Greater semantic engagement relative to phonological rehearsal was hypothesized for 1) sentences vs. word lists, 2) concrete vs. abstract sentences, and 3) well recalled vs. poorly recalled sentences. During auditory perception and the memory delay period, we found highly left-lateralized activation in the form of 8–30 Hz event-related desynchronization. Compared to abstract sentences, concrete sentences recruited posterior temporal cortex bilaterally, demonstrating a neural signature for the engagement of visual imagery in sentence maintenance. Maintenance of arbitrary word lists recruited right hemisphere dorsal regions, reflecting increased demands on phonological rehearsal. Sentences that were ultimately poorly recalled in the post-test also elicited extra right hemisphere activation when they were held in short-term memory, suggesting increased demands on phonological resources. Frontal midline theta oscillations also reflected phonological rather than semantic demand, being increased for word lists and poorly recalled sentences. These findings highlight distinct neural resources for phonological and semantic maintenance, with phonological maintenance associated with stronger oscillatory modulations.

Introduction

Short-term memory (STM) for verbal information has been intensively studied for decades, but debates persist about how many different mechanisms are required to account for human performance. Much research has focused on phonological STM (pSTM), particularly the phonological loop, responsible for subvocal rehearsal of verbal sequences. Although pSTM is indispensible for maintenance of arbitrary information such as digit strings, many theorists believe that other mechanisms supplement pSTM, including semantic resources. A classic task thought to rely on both phonological and semantic resources is sentence repetition, in which subjects hear a sentence and then attempt to repeat it after a brief delay, during which rehearsal may be blocked by dual task demands. Subjects can accurately repeat sentences greatly exceeding their memory span for arbitrary word lists (Brener, 1940), illustrating the advantage afforded by semantic content. Studies of patients with focal lesions have illustrated a double dissociation between phonological and semantic contributions to sentence repetition, implying that they are implemented in separate regions of the brain (Baldo et al., 2008; Butterworth et al., 1990; Belleville et al., 2003; Martin and He, 2004; Martin et al., 1994).

The neural structures responsible for phonological and semantic resources in sentence repetition are not completely understood. Neuroimaging work has suggested that regions of the posterior parietal and dorsolateral prefrontal cortices play a key role in pSTM (Linden, 2007), but the neural correlates of semantic resources have proven

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more elusive. Some theorists posit a dedicated mechanism for short-term semantic maintenance, termed "semantic STM" (Martin and He, 2004) or "conceptual STM" (Potter and Lombardi, 1990), and imaging studies have suggested that this mechanism may depend on structures also implicated in semantic processing in general, including ventral regions of the left inferior frontal gyrus (LIFG, e.g. Brodmann areas 45/47) and middle temporal gyrus (Shivde and Thompson-Schill, 2004; Hamilton et al., 2009). Other theorists argue that semantic STM is a manifestation of long-term memory (LTM) processes operating over a short time scale (Cameron et al., 2005; Ruchkin et al., 2003), in which case one might expect the involvement of medial temporal lobe structures.

It is increasingly recognized that the major brain networks involved in language and verbal memory are also found in non-human primates, and presumably also subserve functions other than language. In the last decade, the ventral stream / dorsal stream dichotomy previously recognized in vision and audition ("what" vs. "where" pathways) has also been applied to language (Hickok and Poeppel, 2007; Saur et al., 2008). A dorsal pathway links posterior superior temporal cortex to the IFG (BA 44/45) via the superior longitudinal fasciculus, and is thought to subserve phonological and syntactic functions, including speech production and possibly pSTM. A ventral pathway extends the length of the temporal lobe, crossing into ventral IFG via the extreme capsule and uncinate fasciculus, and is implicated in semantic processing. Language comprehension is thought to occur in the ventral pathways of both hemispheres, while speech production is strongly left-lateralized. Additionally, an even more dorsal pathway linking the parietal lobe and dorsolateral prefrontal cortex (DLPFC) is thought to contribute to domain-general resources in STM, including maintenance of serial order information in verbal recall (Majerus, 2013). This dorsal-frontal parietal circuit is commonly activated in fMRI studies of verbal working memory emphasizing rote rehearsal through the use of arbitrary stimuli such as lists of numbers or letters (Linden et al., 2007). Studies of semantic maintenance have typically revealed activation in more ventral regions (see above), consistent with a dorsal/ventral dichotomy of the respective phonological and semantic resources that may be involved in sentence repetition. In the present study, we hypothesized that phonological maintenance would selectively engage dorsal stream structures, and semantic maintenance would engage ventral stream structures.

Besides being dissociated in terms of the brain regions recruited, distinct forms of short-term memory may recruit different forms of neural activity reflected in modulations of oscillatory power in distinct frequency bands, including theta (4–7 Hz), alpha (8–12 Hz), beta (15–30 Hz), and gamma (> 40 Hz) bands. Studies of verbal short-term memory using EEG and MEG have shown increasing memory load during a delay period can induce increased power in theta (Jensen and Tesche, 2002; Zakrzewska and Brzezicka, 2014), alpha (Jensen et al., 2002; Grimault et al., 2009), and gamma (Howard et al., 2003; Meltzer et al., 2008) bands, although other studies have also shown that power in these frequency bands may instead be negatively correlated with memory load in some circumstances (Gevins et al., 1997; Meltzer et al., 2007). Intracranial EEG data has shown that different brain areas can respond to memory load with power changes in opposite directions, (Meltzer et al., 2008), highlighting the importance of spatial localization of power changes rather than considering each frequency band as a monolithic entity. The study of oscillatory activity using MEG during a memory delay period is advantageous in that the activity can be unambiguously attributed to the memory delay, as opposed to the initial encoding of the verbal stimuli into short-term memory. In functional MRI studies of short-term memory, the delayed hemodynamic response results in greater overlap of activity attributable to encoding and subsequent maintenance.

The present study aimed to assess the contributions of distinct brain regions and distinct oscillatory reactivity patterns in sentence repetition, using source-localized MEG data acquired in the context of three experimental manipulations designed to control the degree to which semantic resources were involved. First, we compared sentences to word lists, which have minimal semantic content and therefore tax pSTM heavily. The lack of semantic support for word list memory likely accounts for the much longer memory span that healthy subjects have for sentences compared to word lists. In this study, we chose the length of the sentences and word lists based on prior literature in an attempt to achieve approximately equal accuracy in short-term recall for both stimulus types. Using Alan Baddeley's estimate that "Memory span for unrelated words is around 5, increasing to 15 when the words make up a sentence" (Baddeley, 2012), we chose a length of 5 for word lists, and an average length of 13 words for sentences, taking into account other factors affecting the difficulty of sentence recall (see below). By directly comparing these two conditions which were roughly equated in performance (see behavioural results below), we reasoned that word lists would engage pSTM to a greater extent than sentences, whereas the opposite would be true for semantic resources.

Second, we compared concrete vs. abstract sentences, expecting more semantic engagement with concreteness. This manipulation is based on several prior studies showing improved recall for word lists comprising concrete words (Bourassa and Besner, 1994; Walker and Hulme, 1999; Miller and Roodenrys, 2009), as well as our prior behavioural study with the same materials showing a strong advantage for concrete relative to abstract sentences (Meltzer et al., 2016). We reasoned that the improved recall is attributable to greater engagement with existing semantic representations, and that brain regions involved in semantic processing may therefore be more highly activated when holding concrete sentences in STM relative to abstract sentences, despite the greater difficulty of abstract sentence recall.

Third, we compared sentences based on how well they were recalled in a post-test, reasoning that sentences that were better encoded into LTM would have benefited from deeper semantic processing during their initial maintenance period. This prediction arises from the literature on "levels of processing," stemming from the finding that making a semantic decision about a word promotes greater encoding of that word into LTM relative to a perceptual or phonological decision (Craik and Lockhart, 1972). In our prior behavioural study (Meltzer et al., 2016), we found that interfering with pSTM through articulatory suppression during the delay period of a short-term recall task actually improved the retention of sentence content in LTM, assessed by subsequent surprise cued recall, suggesting that suppressing pSTM increased the compensatory engagement of semantic maintenance processes. In the present study, we applied the same cued recall procedure to classify sentences posthoc as well encoded or poorly encoded, and compared neural activity during maintenance of both categories of sentences. Although in the present study we did not attempt to deliberately suppress pSTM, we reasoned that greater engagement of semantic maintenance would promote encoding, and thus greater activation of the relevant structures might be seen during the maintenance of sentences that were ultimately well remembered. Similarly, we hypothesized that poorly-encoded sentences would involve greater activation of structures involved in pSTM, reflecting a "rote rehearsal" strategy that does not promote long-term encoding.

In order to fully distinguish between activity related to perceiving the sentence and holding it in memory, we analyzed oscillatory activity specifically during the memory maintenance period using magnetoencephalography (MEG), which instantaneously measures neuronal activity without the confound of hemodynamic delay that complicates fMRI studies of memory maintenance.

Materials and methods

Participants

Twenty-five right-handed, healthy adults participated in the experiment (13 males; mean age = 23.92 ± 3.3 years). Participants were