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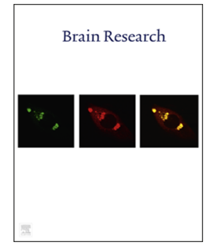


Review

# What works in auditory working memory? A neural oscillations perspective

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ABSTRACT

Working memory is a limited resource: brains can only maintain small amounts of sensory input (memory load) over a brief period of time (memory decay). The dynamics of slow neural oscillations as recorded using magneto- and electroencephalography (M/EEG) provide a window into the neural mechanics of these limitations. Especially oscillations in the alpha range (8–13 Hz) are a sensitive marker for memory load. Moreover, according to current models, the resultant working memory load is determined by the relative noise in the neural representation of maintained information. The auditory domain allows memory researchers to apply and test the concept of noise quite literally: Employing degraded stimulus acoustics increases memory load and, at the same time, allows assessing the cognitive resources required to process speech in noise in an ecologically valid and clinically relevant way. The present review first summarizes recent findings on neural oscillations, especially alpha power, and how they reflect memory load and memory decay in auditory working memory. The focus is specifically on memory load resulting from acoustic degradation. These findings are then contrasted with contextual factors that benefit neural as well as behavioral markers of memory performance, by reducing representational noise. We end on discussing the functional role of alpha power in auditory working memory and suggest extensions of the current methodological toolkit.

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## 1. Introduction

It is of great use to any behaving organism to be able to retain some internal representation of fleeting sensory input, at least over short periods of time. A limited-capacity, limited-duration memory system provides such independence from sensory input and arguably enables complex cognitive functions like reasoning or discourse. This attractive design feature is, in essence, what we will here refer to as short-term (or "working") memory.

Short-lived and time-critical memory functions are all the more fascinating in the auditory domain. Here, the sensory input itself – sound – is a function of time and requires tens to hundreds of milliseconds (for a syllable or a word, respectively) to develop acoustically and to become neurally encoded. In the laboratory, we break this memory process down into simple tasks such as the neural encoding of a complex yet inherently meaningless sound, holding it in "working memory" for a brief period, only to compare it against another (or identical) complex sound (Kaiser et al., 2009; Scott et al., 2014; Wilsch et al., 2015a). However, such artificial and controlled settings should not detract from the real-life relevance of auditory working memory and its limitations, which for example gain notoriety in people coping with hearing loss. But let us begin by outlining the defining features of working memory, and some of its specifics in audition. We will then go on to present evidence on what magneto- and electroencephalography (M/EEG) and in particular studies on the role of neural oscillations have taught us about auditory working memory thus far.

As argued above, working memory is constitutional to our cognitive system. It serves as an interface between perception, long-term memory, and action (Baddeley, 2003). Despite the physical absence of the sensory input, a representation of the information can be maintained and manipulated (i.e., "worked" with) over a brief period of time (Baddeley, 2012). It is a defining feature that the cognitive resources constituting working memory are limited with regard to the load of information that can be maintained (i.e., memory load) as well as to the duration of how long information can be maintained (i.e., memory decay). These constraints are inherently linked to the limited amount of attention that can be allocated to the to-be-remembered information (Gazzaley and Nobre, 2012). When limitations are exceeded, performance declines due to a lack of attentional resources (Norman and Bobrow, 1975).

The limitations of working memory have been widely discussed and studied. In brief, limitations can be observed at three stages: encoding, maintenance, and retrieval of the information entering memory (Baddeley, 2012). From a cognitive-processes point of view, we will here focus on encoding and maintenance of auditory information; that is, perceptual processing of information in the focus of attention and the subsequent protection of the memory representation from disrupting, irrelevant information (Postle, 2006). From a neural-processes view, we will deliberately focus on the particular role of neural oscillations and how they are thought to support these cognitive processes.

## 2. A brief reminder on memory load

Traditionally, the term memory load referred to the number of items to be held in working memory. Miller (1956) was the first to postulate $7 \pm 2$ items as the maximum load that can be stored in working memory characterizing memory capacity. Later, this number has been revised to only four items (Cowan, 2001).

As outlined in greater detail in a section below, evidence from neural oscillations especially in the alpha frequency band (8–13 Hz) supports the notion of parametric increase in memory demand and allocated neural resources: first, alpha power increase has been observed during working memory maintenance per se (e.g., Busch and Herrmann, 2003; Haegens et al., 2010; Jokisch and Jensen, 2007; Kaiser et al., 2007a; Luo et al., 2005; van Dijk et al., 2010a). Second, alpha power has been repeatedly found to increase parametrically with memory load, such as number of items (Jensen et al., 2002; Leiberg et al., 2006b; Obleser et al., 2012).

The so-called "slot models" of working memory are in line with memory capacity limits based on item number. These models assume that each item is stored in a slot in memory until all slots are filled (Zhang and Luck, 2008). All of these items are then maintained with equal precision (for a review see Alvarez and Cavanagh, 2004; Fukuda et al., 2010; Luck and Vogel, 1997).