Brain Research

## 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).

However, recent behavioral as well as neural studies have shown convincingly that the acuity of memory performance parametrically declines and alpha power (see above) parametrically increases with an increasing number of items (Wilken and Ma, 2004; Ma et al., 2014). This implies that, without exceeding the capacity limits, the acuity of memory representations and the number of distinct items in memory depend on each other.

Thus, a new family of working memory models that focuses on the use of limited resources has been proposed (for a review see Ma et al., 2014). These so-called "resource models" assume that representations in memory are always and inevitably noisy and that the noise increases with increasing memory load (Bays and Husain, 2008; Wilken and Ma, 2004). Noise is understood to be inherent to the cognitive system, but note that this 'noise' concept makes these models particularly attractive to be applied in the auditory domain, where external noise as well as internal noise (e.g. degraded sensory encoding in various forms of hearing loss) are salient. The concept of noise put forward in resource models of working memory is based on random (neuronal) fluctuations that impede a perfect mapping of sensory information onto memory. Further, and in line with sensory gain theories of attention, it is posed that this noise can be reduced by allocating more attentional resources. The various resource models agree that the total amount of available resources is limited but the number of items that can be represented in memory is not. However, the greater the number of items in memory, the higher the degree to which neural resources need to be divided amongst items. This in turn results in less precise memory representations.

The concept of precision is based on the idea that distinct information stored in working memory elicits firing of distinct neural populations in sensory cortices (Ester et al., 2013). However, when the distinctiveness of items in memory is reduced, for example due to increased memory load (Kumar et al., 2013) or due to similarity among the stored items (Awh et al., 2007), neural responses are more unspecific. The neural noise increases (Bays, 2014), and consequently memory acuity decreases.

Taking the concept of noise quite literal, the remainder of this review will focus on the encoding and maintenance of auditory information. Audition and in particular the processing of speech become demanding for the listener as soon as acoustic degradation (i.e., environmental noise, competing talkers) or auditory degradation (i.e., the lack of precision in neural encoding that accompanies sensorineural hearing loss, Bernstein and Oxenham, 2006; Humes and Roberts, 1990) is introduced. Behaviorally, the degradation of speech signals through an added noise masker has been shown to increase memory load and to decrease memory performance (for a review see Pichora-Fuller and Singh, 2006; Pichora-Fuller et al., 1995; Rudner et al., 2011). Note that this increase of memory load is in line with the above-cited resource models of working memory: due to additional resources required for processing degraded speech, less resources are available, memory representations will inevitably be noisier (i.e., less precise) and memory load will increase. Moreover, noisy input such as degraded speech lacks precision by its very nature. This precludes optimally precise representations

in working memory. We will get back to the effect of noise in working memory in Section 5.3.

## 3.　A brief reminder on memory decay

Working memory is not only limited by the amount of information that can be maintained but also by the duration of information maintenance. This is also especially true in the auditory domain. The longer items are stored in working memory the poorer is the memory acuity reflected by a decrease in memory task performance (Ebbinghaus, 1885; for a review see Ricker et al., 2014). According to the memory trace decay theory (Brown, 1958), sensory information leaves a memory trace (i.e., a memory representation) which fades out over the passage of time (Posner and Keele, 1967). The loss of the memory representation is therefore assumed to be a consequence of the amount of time that has elapsed (Cowan et al., 1997). Somewhat in contrast, Barrouillet and colleagues in their Time-Based Resource-Sharing model (TBRS; Barrouillet et al., 2004) claim that time per se is not the factor that causes forgetting. Instead, attentional resources focused on the memory representation are able to counteract decay by means of refreshing the representations (see also Barrouillet et al., 2007). Hence, memory decay depends on the balance of decay over time and attentional resources that refresh the memory representations.

Unfortunately, there is only little direct neural evidence on memory decay. However, a few studies have reported a decline in neural activation with decay. For instance, single-cell recordings of monkeys' neural activation decreased throughout the delay phase of a short-term memory task Fuster, 1999. Similarly, Jha and McCarthy (2000) found a decline in the BOLD response of posterior regions during the visual memory delay phase. One auditory fMRI study on pitch memory reported bilateral supramarginal gyrus (SMG, BA40) to be activated throughout the delay phase and was interpreted as reflecting the maintenance of pitch, accordingly: In left SMG, activation decreased with the passage of time reflecting memory decay (Gaab et al., 2003).

Auditory sensory memory enables integration of auditory information and preservation of information such as sound features over brief periods of time (for a review see Schröger, 2007; Schröger et al., 2014). Accordingly, most evidence on memory decay in the auditory domain has been assessed for sensory memory using the mismatch negativity (MMN), a negative-going event-related potential measured with EEG or MEG (for a review see Näätänen, 2000). In a typical MMN design, the standard sounds are thought to form a memory trace or "central sound representation" from which a deviant sound differs and hence elicits an MMN. This way, the MMN can also serve as an indicator for memory decay: a decreased MMN can be interpreted as a marker for the deterioration of a sensory memory trace with the passage of time.

One of the reasons for stronger decay in sensory memory compared to working memory is that non-verbal or pre-lexical stimuli (Obleser and Eisner, 2009) preclude rehearsal during stimulus maintenance (Cowan, 1984; Cowan et al., 1997; Cowan and AuBuchon, 2008; Keller et al., 1995; McKeown and Mercer, 2012). See Table 1 for a distinction of

| Table 1 – Auditory short-term memory. | |
| --- | --- |
| **Auditory working memory** | |
| Characteristics | Post-categorical/"phonological" level (see Obleser and Eisner, 2009) |
| | Storage and manipulation of representation of auditory-verbal information over a brief period of time (Baddeley, 2012) |
| | Interface between perception, long-term memory, and action (Baddeley, 2003) |
| | Maintenance of only a limited amount of information |
| | Information stored in memory decays slowly, counteracted by rehearsal |
| Oscillatory parameters | Alpha power fluctuations during stimulus maintenance: |
| | • Increase with increasing number of items: posterior parietal sensors (Leiberg et al., 2006b) |
| | • Increase with increasing degradation: right superior parietal cortex, right SMG, right STG, Precuneus (Obleser et al., 2012) |
| | decrease when degraded syllables are temporally expected (symbolic cues): right insula (Wilsch et al., 2015a) |
| | • Decrease when clear syllables are temporally expected (longer foreperiod duration): right fronto-temporal sensors (Wilsch et al., 2015b) |
| | decrease with increasing predictability of probe stimulus (S2): centro-parietal (Wöstmann et al., 2015) |
| | Gamma power increase during stimulus maintenance: |
| | • Increase in spatial short-term memory: left parietal sensors (Kaiser et al., 2009; Leiberg et al., 2006a; Lutzenberger et al., 2002) |
| | • Increase compared to control task: left inferior frontal and anterior temporal (Kaiser et al., 2003) |
| **Auditory sensory memory** | |
| Characteristics | Pre-categorical/sensory level (see Obleser and Eisner, 2009) |
| | Integration of auditory information and preservation of information such as pre-lexical sound features over brief periods of time (Schröger, 2007) |
| | Maintenance of only a limited amount of information |
| | Fast decay because rehearsal is not possible: early sensory store that lasts between 100 and 300 ms and a longer store where auditory information can be stored up to ten seconds (Cowan, 1984) |
| Oscillatory parameters | Alpha power increase during stimulus maintenance compared to control: left temporal brain regions (van Dijk et al., 2010a) |
| | Gamma power increase during stimulus processing (i.e., match-and-utilization model; Herrmann et al., 2004; Debener et al., 2003): |
| | • Early enhanced gamma (before 150 ms after stimulus onset) reflects matching of bottom-up signals with memory contents |
| | • Late gamma response (after 200 ms after stimulus onset) reflects utilization processes: reading out the match/mismatch leading to up dating of the memory contents, behavioral responses, or reallocation of attention |

working memory versus sensory memory. Most relevant to the present paper's main focus, however, we are not aware of published findings on the modulation of neural oscillations by (sensory) memory decay.

It remains to be shown how human neuro–cognitive resources, despite their limitations, render maintenance and manipulation of encoded sound information possible. This will be the subject of the remainder of this paper.

## 4. Neural oscillations in auditory working memory – a special role for alpha?

Neural oscillations are a viable candidate measure in order to assess the underlying neural mechanisms that enable and control memory load and memory decay. Oscillatory fluctuations in frequency bands of the local field potential (LFP, as measured using invasive electrophysiology) or in scalp voltage or magnetic flux (using EEG or MEG, respectively) are thought to reflect a regime of "brain states" that control the flow of information between neurons and neuronal populations (which inturn is thought to be mainly expressed in the "output" of neurons, that is, in neuronal firing; e.g., Lakatos et al., 2008; Kayser et al., 2012; Buzsáki, 2006).

With respect to working memory maintenance, neural oscillations in the theta (~4–8 Hz), alpha (~8–13 Hz), and gamma (~30–200 Hz) frequency range have all been reported to vary in magnitude with working memory load (see Table 1; for a review see Roux and Uhlhaas, 2014; Jensen, 2006). Since the focus of the present review is on alpha-power fluctuations in working memory, let us only briefly summarize the role of theta and gamma power: Due to their prominent role in hippocampal circuitry, theta oscillations are at the heart of many neural models of memory (Lisman and Buzsáki, 2008; Lisman and Idiart, 1995). Theta power has been repeatedly found to increase with working memory load (Raghavachari et al., 2001; Jensen et al., 2002; Moran et al., 2010). Specifically, theta oscillations have been associated with the sequential aspects of memory content (Buzsáki, 2002; Hsieh et al., 2011; Lisman, 2010; Lisman and Jensen, 2013), much akin to the classic Sternberg paradigm (Sternberg, 1966). Gamma power, conceptualized to occur nested within slower cycles of theta, has been reported to increase during working memory maintenance of visual (Tallon-Baudry et al., 1998; Medendorp et al., 2007; Jokisch and Jensen, 2007; Roux and Uhlhaas, 2014), auditory (Lutzenberger et al., 2002; Kaiser et al., 2007b, 2009), and somatosensory (Haegens et al., 2010)

stimuli, presumably reflecting active maintenance of working memory representations.

We will now focus in more detail on recent evidence on how alpha power can reflect memory load in auditory working memory. The alpha frequency band (traditionally defined as 8–12 Hz, often liberally extended to ~7–14 Hz) dominates the spectrum of human neural oscillations (Berger, 1929). Alpha power is indicative of a variety of cognitive states and functions, all predominantly related to attention – of which memory maintenance arguably is a sub-process (see Gazzaley and Nobre, 2012; for broader views on potential roles of alpha in audition, see e.g. Weisz et al., 2011 and Strauß et al., 2014).

Within the framework of the "functional inhibition" hypothesis, it is assumed that higher alpha power during item retention in working memory reflects the inhibition of task-irrelevant sensory input and/or task-irrelevant neural processes (for review see Klimesch, 2012) and/or brain regions (for review see Jensen and Mazaheri, 2010). In line with this concept of functional inhibition, studies on visual working memory reported increased alpha power, emerging from visual brain regions, which was interpreted to reflect the inhibition of sensory processes during memory maintenance (Jensen et al., 2002; Tuladhar et al., 2007). Comparable effects have been found in the auditory modality where alpha power was increased in the right hemisphere inhibiting active pitch processing during a pitch-discrimination task (van Dijk et al., 2010b) as well as for somatosensory working memory where alpha power was shown to be increased over primary somatosensory cortices in the ipsilateral (irrelevant) hemisphere (Haegens et al., 2010; Whitmarsh et al., 2014). As hinted above, it has been demonstrated in the macaque brain that alpha activity drives neuronal spiking, and that alpha power is associated with the spike rate during maintenance of a somatosensory stimulus, which supports an inhibitory, or more generally, controlling role of alpha power (Haegens et al., 2011).

However, it remains to be shown how inhibitory control through alpha power is modulated in response to acoustic challenges and the concomitant increased memory demands.

### 4.1. How does alpha power reflect memory demands due to acoustic signal degradation?

In the auditory domain, the maintenance of non-degraded information in working memory increases alpha power (Leiberg et al., 2006b; Luo et al., 2005; van Dijk et al., 2010b). Thus, even negligible levels of memory load (e.g., storing a single, non-degraded syllable) allocate alpha power. This is reminiscent of the long known fact that attention to the auditory modality increases parieto-occipital alpha power (Adrian, 1944) and leads to the following question: How will further acoustic signal degradation, as it commonly occurs in every listener's environment, affect this alpha allocation process? As argued above, noisy physical stimuli reduce encoding precision and thus demand more attentional resources during stimulus maintenance. In short, degraded acoustic information increases memory load (Pichora-Fuller and Singh, 2006). While not focusing on memory in particular, Strauß et al. (2014) have recently suggested a framework for alpha power as a tool for attentional selection under adverse listening conditions. We here posit that the demands of attending to a degraded *physical* stimulus versus attending to the *memory representation* of a degraded stimulus trigger the same neural compensatory mechanisms.

Following this framework, a recent study by Wöstmann et al. (2015) investigated the impact of degraded speech on alpha power during stimulus encoding in a delayed matching-to-sample task. They reported a parametric increase of parieto-occipital alpha power with reduced acoustic detail. This effect was observed during the encoding of both critical stimuli (Fig. 1A). These findings are in line with a previous study by Obleser et al. (2012) who reported a parametric increase of alpha power during encoding of degraded speech but, in particular, also during maintenance of these speech signals (Fig. 1B). A source localization of this degradation- and load-driven alpha increase revealed precuneus and posterior cingulate as primary origins. Similar to the parieto-occipital topography of Wöstmann et al. (2015), these sources have been shown before to inhibit task-irrelevant processes in a top-down fashion (Klimesch et al., 2007; Jensen and Mazaheri, 2010). In addition, supramarginal gyrus (SMG) and the right temporo-parietal junction, both previously reported to play an essential role during verbal working memory (Paulesu et al., 1993; Obleser and Eisner, 2009), contributed to this alpha enhancement.

As mentioned before, neural oscillatory data on memory decay are sparse. However, preliminary data from an auditory sensory memory task (one representative participant, see Fig. 1C) indicate a decrease of alpha power with longer maintenance intervals at occipito-parietal areas. It is tempting to interpret this alpha power decrease as a decrease of functional inhibition in task-irrelevant visual areas: In line with memory decay theory (see Brown, 1958), a "fading away" of the auditory sensory representation would require less inhibition of potentially interfering processes by means of alpha power.

As these studies have shown that acoustic degradation is accompanied by alpha power increase, can we find evidence on factors that counteract memory load and memory decay and consequently modulate the respective oscillatory markers in the alpha range?

### 4.2. Which factors counteract memory load and memory decay?

In line with resource models of working memory, degraded acoustic information leads to a noisier working memory representation (see above; Ma et al., 2014). A noisier representation demands more cognitive resources in order to be successfully maintained. Hence, memory load increases, which is reflected by increased alpha power during the delay phase. However, in everyday life situations, listeners are able to successfully process and store degraded speech nevertheless. The question arises whether the listeners' use of potentially beneficial information might increase encoding precision and consequently reduce memory load.

We have thus far collected evidence on the beneficial (and thus alpha power-modulating) role of three such factors: explicit temporal expectations, implicit temporal expectations, and semantic predictiveness.
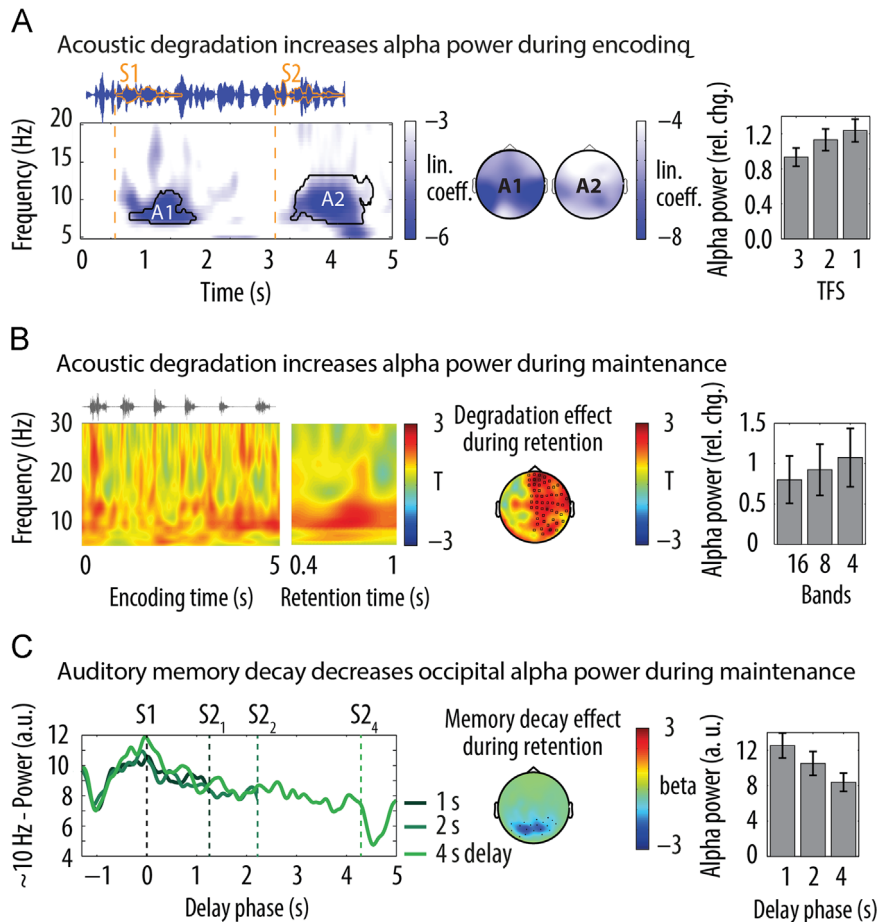
Fig. 1 – Alpha power fluctuations in auditory working memory. (A) Parametric increase of oscillatory power in the alpha range (see time–frequency plot, A1 and A2 clusters) with decreasing acoustic detail (i.e., amount of temporal fine structure) during encoding of the first (S1) and the second numeral (S2; figure adapted from Wöstmann et al., 2015). Topographies display scalp distribution of the beta values describing the statistical effect in two separate clusters (A1 and A2). (B) Parametric increase of right-lateralized alpha power (~10 Hz) with increasing acoustic degradation during stimulus retention (figure adapted from Obleser et al., 2012). A decreasing number of noise-vocoded frequency bands increases acoustic degradation. Concomitantly, degradation induces memory load reflected by alpha-power increase. (C). Data of one exemplary participant representing parametric decrease of occipito-parietal alpha power (8–13 Hz) with increasing retention phase duration (unpublished data). Plotted lines illustrate alpha power averaged across sensors displayed in topography. Each line represents alpha-power decrease for each delay phase duration (1, 2, 4 s). Topography displays beta values describing the slope of alpha power decrease estimated before S2 of each delay phase condition.

A first potential means to improve encoding precision could be the a priori formation of temporal expectations for a stimulus (e.g., Rohenkohl et al., 2012). In the auditory domain, we recently investigated the impact of explicit temporal expectations on the memory maintenance of syllables presented in noise (Wilsch et al., 2015a). Participants performed a delayed matching-to-sample task and symbolic cues informed about the time-of-occurrence of the to-be-remembered syllable. Informative cues did not only improve working memory performance, but also reduced alpha power during stimulus maintenance (Fig. 2A). This alpha power effect emerged from the right insula, a major hub of the cingulo-opercular network, which has been been argued to be responsible for sustained task-related cognitive control (Dosenbach et al., 2007).

Also, we investigated the effect of explicit temporal expectations on memory decay. Participants had to maintain sound sequences presented in noise in memory for one, two, or four seconds. These to-be-remembered sequences followed either a temporal cue indicating that the to-be-remembered sound sequence would occur always at the same point in time after cue onset (i.e., fixed foreperiod duration inducing explicit temporal expectations) or a temporal cue indicating that the time point of stimulus occurrence would vary (i.e., jittered foreperiod duration inducing no explicit temporal expectations). Preliminary data show that behavioral performance decreased less with longer maintenance when foreperiod durations were fixed. Temporal expectations also had an impact on alpha power: for fixed foreperiod durations, alpha power stayed at level for each delay phase duration. When the foreperiod was jittered, alpha power decreased with increasing delay phase duration. The difference in alpha power decline between fixed and jittered foreperiods emerged from left lateralized brain sites,
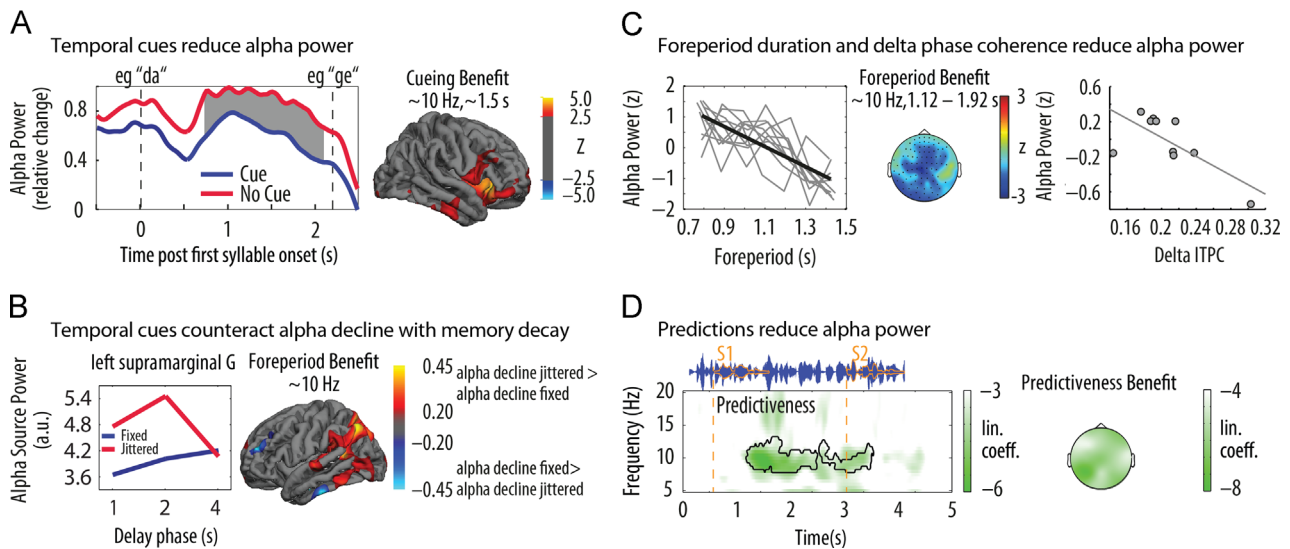
**Fig. 2 – Alpha power modulations through beneficial effects on memory load and memory decay.** (A) Alpha power (8–13 Hz) increases during retention when spoken syllables are presented in noise reflecting increased memory load (figure adapted from Wilsch et al., 2015a). A priori temporal expectations by means of symbolic cues counteract memory load and reduce alpha power. This effect emerges from the right insula. (B) Data of one exemplary participant showing alpha power decrease the longer degraded acoustic information is stored in auditory sensory memory (red line; unpublished data). Temporal expectations by means of fixed onset-times of the to-be-remembered stimuli counteract this decline in alpha power (blue line). The effect emerges from left supramarginal gyrus and left visual areas. (C) When syllables are presented clearly, alpha power during stimulus retention decreases with temporal expectations implicitly induced by longer foreperiods (i.e., hazard function; figure adapted from Wilsch et al., 2015b). In addition, increased delta ITPC during stimulus presentation correlates negatively with alpha power during retention, providing the direct link between improved stimulus encoding and subsequent reduction of memory load. (D) Alpha power decrease with increasing semantic predictability in a number comparison task (figure adapted from Wöstmann et al., 2015). Effect occurs after presentation of the first numeral and before presentation of the second numeral, at the time when the prediction is formed. Black lines in time–frequency plot mark temporal dimension across frequencies, topography indicates spatial distribution across electrodes.

centered on supramarginal gyrus (see data of one exemplary participant in Fig. 2B). These results tentatively suggest that explicit temporal expectations counteract not only memory load but also memory decay.

Second, the same experiment as conducted by Wilsch et al. (2015a, see above)but without noise allowed us to investigate the effect of temporal expectations at a very low level of memory load (Wilsch et al., 2015b). Here, symbolic cues did not impact alpha power during stimulus maintenance. However, since the interval between cue offset and stimulus onset (i.e., foreperiod) was jittered, temporal expectations were induced more implicitly across the experiment based on the passage of time (i.e.,'hazard function'; Nobre et al., 2007). Hence, longer foreperiods increased temporal expectations which in turn led to reduced alpha power during stimulus maintenance at central sensors (see Fig. 2C). Moreover, longer foreperiods increased slow-delta phase coherence during stimulus encoding, reflecting the neural basis of temporal expectations and its facilitating effect on stimulus encoding. The connection of both effects was expressed in a negative correlation of delta phase coherence during stimulus encoding and alpha power during stimulus maintenance: independent of foreperiod duration, improved encoding (delta phase coherence) led to a reduction of memory load (alpha power; see Fig. 2C).

Third, and going beyond enhancing encoding precision, Wöstmann et al. (2015) manipulated acoustic degradation and semantic predictiveness in a number comparison task. A spoken digit (ranging between [21; 99]) masked by a speech masker had to be maintained in working memory until a second number was presented. Participants had to indicate whether the second digit was smaller or bigger in numerical value than the first. The further away the first digit was from the numerical center between 21 and 99 (i.e., 60) the higher was the predictiveness of the semantic content of the second digit and consequently of the correct response. Wöstmann et al. (2015) could show that semantic predictiveness reduced alpha power parametrically during stimulus maintenance at centro-parietal sensors (see Fig. 2D).

These data all show that, either during or after stimulus encoding of speech signals in auditory working memory, strategies counteracting memory load take effect. These strategies result in improved memory performance as well as in modulated alpha power.

## 5. Controversies and future directions

### 5.1. The role of alpha power in auditory working memory

In the studies reviewed here, not all alpha power effects emerged from brain sites that are readily interpretable within

a functional inhibition framework. For example, alpha power effects at parieto-occipital sensors as reported by Wöstmann et al. (2015) and Obleser et al. (2012) are in line with the idea that alpha power inhibits irrelevant brain regions. Similarly, the single-participant data on memory decay (Fig. 1B) presenting a decline in alpha power at occipital sensors, most likely emerging from visual areas is most in line with the concept of functional inhibition (Fig. 1C). However, the alpha power effect of temporal expectations in the study by Wilsch et al. (2015a) emerged from the cingulo-opercular network (Fig. 1A). Both, the effect of temporal expectations on memory decay (Fig. 2B) as well as alpha-power increase with increasing signal degradation (Obleser et al., 2012) emerged from supramarginal gyrus, a brain region often found to be actively involved in short-term memory (Gaab et al., 2003; Paulesu et al., 1993). In how far is the involvement of these functional diverse networks compatible with a parsimonious functional inhibition idea?

Initially, an increase in alpha power was explained within the framework of functional inhibition (Jensen et al., 2002; Klimesch et al., 2007), a mechanism that gates the transmission of information through inhibition and activation of brain regions. Inhibition has been argued to be reflected in increased alpha power whereas decreased alpha power enhances neuronal excitability and thus reflects active processing of information.

The strong involvement of "executive" or attention networks implies that alpha power might not just reflect immediate inhibition of the region from where it emerges: the cingulo-opercular network but also the fronto-parietal network (Dosenbach et al., 2007) comprise the executive control systems performing top-down focus of attention most likely enhancing stimulus maintenance. These networks have all been shown before to be active and relevant during working memory maintenance (Leung and Alain, 2011, for reviews see Jonides et al., 2008 and Postle, 2006). Moreover, Sadaghiani et al. (2012) found a positive correlation of alpha power and the BOLD response of the cingulo-opercular network. Therefore, it is not very likely that alpha power emerging from these areas reflects a direct inhibiting mechanism.

Further, based on the findings of Ray and Cole (1985), alpha power has also been interpreted as a marker of internally directed attention and, more specifically, of transmitting information within working memory (for a review see Palva and Palva, 2007). In visual working memory (Palva et al., 2010) showed that alpha power played a major role in the communication between frontal regions underlying maintenance of working memory as well as frontal- and visual regions during stimulus maintenance. Hence, their findings are in line with the interpretation that alpha power from executive control systems reflected the system's top-down enhancing of stimulus maintenance.

Now, returning to the framework of functional inhibition, most of these findings supporting direct inhibition are based on alpha power emerging from sensory regions (e.g., Haegens et al., 2010; van Dijk et al., 2010b; Jensen et al., 2002; Whitmarsh et al., 2014). The data of the exemplary participant (Fig. 1C) show that alpha power declining with memory decay emerged from V1 and is indeed most likely to reflect

inhibition of this task-irrelevant sensory area. However, the reported localizations of alpha power are also partially in line with claims from Palva and colleagues.

Increased alpha power during memory maintenance appears to be more than just an epiphenomenon of short-term memory. In different sensory modalities alpha power has been shown to correlate positively with memory performance (Hanslmayr et al., 2005; Haegens et al., 2010; Wilsch et al., 2015a; Wöstmann et al., 2015) and hence appears to be beneficial for working memory processes. At the same time, due to the presumably inhibitory effect, increased alpha power correlates negatively with perceptual performance (Ergenoglu et al., 2004; Hanslmayr et al., 2007) and vice versa, decreased alpha power enhances active sensory processing (for a review see Palva and Palva, 2007; Hanslmayr et al., 2012).

Thus, it seems as if the summarized alpha power fluctuations during stimulus maintenance represent complex network activity of internally directed attention that enhances working memory processes via active top-down modulations of sensory areas. In sensory areas, either the representation of the stimulus in memory is enhanced or irrelevant areas in an auditory memory task such as V1 are functionally inhibited. Connectivity analyses (Hipp et al., 2011, 2012; Müller and Weisz, 2012; see also section below) will provide necessary information that could actually support or reject this interpretation.

One might ask how the presently discussed active role of alpha power fits the overall notion that alpha power increases throughout an experiment and reflects fatigue? According to Ray and Cole (1985), increased alpha power enhances the focus of attention towards internal mental representation and at the same time inhibiting perceptual processing of external sensory information (see above for alpha power increase/decrease with regards to memory and perceptual processes; see also Palva and Palva, 2007). This mechanism may parsimoniously account for both, maintenance of a memory representation as well as decreased susceptibility to external information, for example with increased fatigue or drowsiness when transitioning to sleep (e.g., first sleep stages or beginning coma being reflected by increased alpha power; Cantero et al., 2002; Supp et al., 2011; not to be confused with sleep spindles, an oscillatory marker for the second sleep stage in the alpha frequency range, for a review see Steriade, 2005). Of course EEG sensor data alone renders it difficult to disentangle whether there are different generators underlying these two alpha phenomena.

## 5.2. Neurobiology of alpha oscillations

As seen in the previous section and throughout the reviewed results, alpha oscillations present effects at a variety of brain sites throughout the cognitive process of encoding and maintaining information in auditory working memory. As discussed earlier, this variety makes it difficult to pinpoint the specific functional role of alpha power. One approach to elaborate on the functional role of alpha power is by considering the neurobiology of alpha oscillations.

How alpha oscillations are neurobiologically initiated and entertained is far from being well understood. The thalamus

has been first discovered as essential generator of alpha power (especially lateral geniculate nucleus; Lopes da Silva et al., 1973). More recent findings also proposed cortico-cortical circuitry (for review see Klimesch, 2012; Lopes da Silva et al., 1980), with both, thalamo- and cortico-cortical generators relying on the intricate layering of neocortex (e.g., Bollimunta et al., 2008; Hughes et al., 2008; van Kerkoerle et al., 2014). A recent paper of Haegens et al. (2015) showed that alpha power generators are present in deeper cortical layers as well as in more superficial layers of different sensory cortices (i.e., visual, somatosensory, and auditory cortices). Haegens and colleagues conclude that alpha power is involved in feedforward and feedback processes. In tune with a role in controlling neural communication, evidence is accumulating that certain ("down") phases of the alpha cycle co-occur with increased firing of neuronal populations (Haegens et al., 2011; Spaak et al., 2012). More specifically, a very recent study by Kayser and colleagues showed, in the rodent, that local field potential oscillations also (but not only) in the alpha range modulate the "response gain" of auditory cortical neurons (Kayser et al., 2015).

Studies at the systems level and computational modeling on alpha generators and the neurotransmitters associated with alpha rhythms provide additional evidence on the functioning of alpha power: it has been shown that metabotropic glutamate receptors (mGluR) and muscarinic acetylcholyn receptors (mAchR) are strongly involved in generating thalamo-cortical alpha power (for review see Hughes and Crunelli, 2005; Hughes et al., 2008). Based on these findings, Vijayan and Kopell (2012) tested a unique conductance-based thalamic model of awake alpha in order to find out whether alpha oscillations serve to process relevant information or rather serve to inhibit irrelevant information, offering an interesting reconciliation: their modeling approach revealed that mAChR-induced alpha power supports processing during a task, whereas glutamergically induced alpha power seems to block unwanted information.

It remains to be seen in how far future methodological advances in non-invasive human neuroimaging (see below) will help to ascribe the observed alpha power changes in EEG/MEG to one or the other of these suggested generators and associated functional roles.

### 5.3. Parallels and differences of sensory degradation in working memory across sensory modalities

In most everyday situations, perceived auditory information is to some degree masked by additional irrelevant information, namely noise. So far, we have discussed how well the limitations of working memory (memory load and memory decay) are suited to study the demanding impact of masking noise on the cognitive system and at the same time we presented evidence on factors counteracting the detrimental effect of noise on auditory working memory.

Although the present review focuses on auditory working memory and auditory noise, it should be mentioned that these detrimental effects of noise are not limited to the auditory domain. External noise in the visual domain such as reduced contrast, superimposed images, or additional irrelevant sensory input has been shown to also increase memory load and thus to interfere with encoding of a stimulus and the maintenance of the memory representation. Moreover, similar to previously summarized findings in the auditory domain, the focus of attention towards relevant features of the to-be-remembered visual information counteracts visual noise in visual working memory (for a review see Gazzaley and Nobre, 2012; Rutman et al., 2010). However, evidence on the facilitating effect of counteracting factors on alpha power in other sensory domains such as visual or somatosensory working memory is sparse. Thus, specificity versus generality of the alpha power mechanisms remains to be delineated. It is a tenable hypothesis that the facilitating mechanism of noise-counteracting factors might be universal across sensory modalities.

### 5.4. Implications of alpha power in auditory working memory for speech and language comprehension

The studies summarized in the present review paper predominantly investigated alpha power fluctuations in young, healthy adults during encoding and maintenance of either clear or degraded sounds, syllables, or single words. These rather low-level stimulations of the normal-functioning brain provide necessary information of basic cognitive functions such as working memory and their corresponding brain signatures. Consequently, findings on this level raise more complex questions that underline the relevance of studying auditory working memory and neural oscillatory responses: What are the implications of alpha power in auditory working memory for more complex listening situations such as speech and language comprehension? Specifically, speech and language comprehension in healthy aging and hearing loss populations will be suited to investigate limitations in auditory working memory and corresponding brain signatures (i.e., alpha power) in an ecologically valid and clinically relevant way.

It is commonly known that speech comprehension becomes more challenging with increasing age: listening to and comprehending speech in noisy environments is very effortful and taxes auditory working memory (Pichora-Fuller, 2003). Accordingly, the Ease of Language Understanding model (ELU; for a review see Rönnberg et al., 2008; Rönnberg, 2003) underlines the relevance of cognitive capacities for language comprehension. Cognitive limitations especially in auditory working memory play an important role when it comes to clinical populations. For example, it has been suggested that working memory capacity is the decisive factor for resultant speech comprehension for people suffering from hearing loss and requiring hearing aids (Rudner et al., 2011; Lunner, 2003). Specifically, increased working memory capacity accounts for benefits from hearing aids (Lunner et al., 2009). Thus, auditory working memory capacities pose a bottleneck for speech comprehension under adverse listening conditions.

To better understand how auditory and cognitive limitations draw on auditory working memory, it is important to study more the relevant brain signatures such as alpha oscillatory dynamics in healthy aging populations (e.g., Wöstmann et al., 2015) and people suffering from hearing loss (Petersen et al., 2015). On the one hand, Wöstmann and

colleagues in their above-referenced study on auditory working memory in a number comparison task (Wöstmann et al., 2015) found that the alpha power dynamics of older listeners are even more sensitive than of younger listeners to the imminent acoustic challenge (i.e., the degradation of the first to-be-encoded digit). This is at least initial evidence that older listeners are not per se limited in their ability to dynamically modulate alpha power depending on task challenges. However, older listeners might nevertheless be too reliant on acoustic or "bottom-up" features rather than adjust their alpha dynamics to "top-down" task requirements (see also Passow et al., 2012).

On the other hand, a recent study on alpha power modulation in an adapted Sternberg paradigm in older hearing-impaired listeners observed that the degree of hearing loss predicted alpha power enhancement during the maintenance phase. Complicating this picture somewhat, however, the highest memory load under acoustically most severe degradation led to a relative *reduction* in alpha power (Petersen et al., 2015). Such an inverted u-shaped alpha pattern shows how sensitively alpha oscillations track the subjective challenges a listener is encountering in auditory working memory tasks; if the challenge exceeded memory capacities in one form or the other, alpha also decreases again (reminiscent of the CRUNCH frame work suggested by Reuter-Lorenz and Cappell, 2008).

In sum, healthy older adults present less hearing acuity, a decreased ability to generate temporal expectations (Zanto et al., 2011), and show altered alpha power dynamics (Petersen et al., 2015; Wöstmann et al., 2015; Zanto et al., 2010). For these reasons it would be most relevant to explore ways how the beneficial factors discussed above (temporal expectations, semantic predictiveness) can be made most salient for older listeners. It is in this respect noteworthy to keep in mind that task- as well as stimulus-driven alpha power modulations are likely to take place simultaneously on at least two levels of processing: More directly in domain-specific, auditory brain regions as well as in domain-general, attention-allocating brain regions such as superior parietal cortex (for discussion see Strauß et al., 2014). Delineating the locus of impairment in older, hearing-impaired listeners will thus also profit from methods that improve on the spatial resolution scalp-recorded EEG.

## 5.5.    *Expanding the methodological scope*

The reviewed findings and remaining open questions call for the employment of different methodological approaches. One question concerns the connectivity of brain regions, the other one considers electrocorticography (ECoG) as a method that provides a great spatial resolution as well as clear signals representing active processing states, and a third approach, brain stimulation, will allow us to test functional models of alpha rhythms in auditory working memory.

### 5.5.1.    *Connectivity analyses*
As outlined above, alpha power effects in auditory working memory emerge from sensory brain regions as well as from different attentional networks. Of course, these regions have differential implications on the functional role of alpha power

in auditory working memory. In order to arrive at a more complete understanding of what alpha-mediated neural communication contributes to working memory, connectivity analyses will be most informative.

Most evidence on connectivity of human brain areas has been accumulated using fMRI and the correlation of the blood oxygen level-dependent (BOLD) signal of different brain regions (e.g., Dosenbach et al., 2007). In contrast to the BOLD signal which just indirectly reflects neural activity (Logothetis, 2008), electro- or magnetophysiological data provide a direct measure of brain activity with a high temporal resolution. For example, Hipp et al. (2012) suggested an approach where orthogonalized source estimates of power in various frequency bands of spontaneous activity were recorded with MEG and correlated.

In a somewhat different approach going beyond spontaneous activity, Weisz and colleagues conducted connectivity analyses of MEG data measured during auditory tasks (Müller and Weisz, 2012; Weisz et al., 2014; Weisz and Obleser, 2014). They projected complex-valued spectral data in the alpha range to source space. Then, phase-locking values, instead of power values, of the regions of interests were calculated, revealing connections between attention networks and primary auditory regions (see also Weisz et al., 2014 for "all-to-all connectivity" and Sporns, 2013 for "small-world" networks). Both approaches would add nicely to the findings reviewed here.

Findings from visual working memory provide evidence on alpha-pulsed long-range connectivity during stimulus maintenance: Pinal et al. (2015) observed long-range connectivity between the alpha phase in right anterior cingulate cortex (ACC) and gamma power (see above) in right supra-marginal gyrus (SMG) as well as right precuneus. The synchronicity between ACC and SMG is indicative of increased activity of the fronto-parietal network during working memory, whereas the connection between ACC and precuneus seems to be of anti-phasic nature. That is neural activity in precuneus is increased when neural activity in ACC is suppressed.

In order to provide more information about alpha oscillations and their functional role during auditory memory, it is necessary to assess the connections of the localized brain regions. In the data reviewed here, alpha power effects of temporal expectations emerged from right frontal sensors and were localized in the cingulo-opercular network. Connectivity analyses could reveal whether the top-down controlling cingulo-opercular network modulates auditory processing in STG directly. Showing such a connection would add evidence to the mode of action of temporal expectations on auditory working memory. Moreover, considering alpha phase, in addition to alpha power, might provide additional information about long-range connectivity between frontal and posterior brain areas and the top-down modulatory effect of alpha oscillations during auditory working memory.

### 5.5.2.    *Electrocorticography*
The spatial resolution of MEG is limited such that source localization techniques can only approximate the actual sources of the signal measured on the scalp. These limitations prevent the analysis of brain responses at their

immediate origin. The precise location of activity, however, provides further insights on the underlying neural mechanisms. Electrocorticography (ECoG), for example, has a higher temporal and spatial resolution ($\sim 4\,mm^2$) than other, non-invasive neuroimaging techniques (Miller et al., 2009). Therefore, ECoG would be very suitable to investigate alpha power fluctuations in auditory working memory in more detail.

Moreover, in an auditory selective attention task, it was shown that attended sounds elicited an increase of high gamma activity in posterolateral superior temporal gyrus (Nourski et al., 2015). Similarly, the effect of temporal expectations could be assessed. When stimuli are expected, the pattern of gamma activity in primary auditory cortices would most likely change, reflecting enhanced processing. In addition, the increased focus of attention could as well be reflected in an increase of gamma power in attentional networks.

Thus, ECoG measures could give rise to a more nuanced perspective on memory load in auditory working memory. For example, the locations of auditory memory representations as well as top-down modulations of these representations through attentional networks could be identified. Presumably, such findings could illustrate a possible "neural" fading out of the memory representation.

### 5.5.3. Brain stimulation

The precise neurobiological grounding of auditory working memory functions in alpha power is so far unclear. Here, brain stimulation approaches such as transcranial magnetic stimulation (TMS) or transcranial electric stimulation with alternating or direct current (tACS/tDCS) will provide further insight. Both methods have been shown to noninvasively manipulate brain oscillations leading to enhancement or suppression of neural oscillations in certain frequency bands, and thereby allow researchers to test the causal relationship between neural oscillations and brain functions (for a review see Hartwigsen, 2014; Thut et al., 2011; Zaehle et al., 2010): TMS can be applied as repeated pulses (i.e., rTMS), while tACS induces a rhythmically alternating electric current, both in specific frequencies.

Since neural oscillations are strongly coupled to cognitive functions, these brain stimulations interfering with oscillations have an impact on cognitive performance (for a review ontACS see Antal and Paulus, 2013; Herrmann et al., 2013). For example, rTMS applied at the individual alpha frequency has been shown to improve cognitive performance (Klimesch et al., 2003) and to enhance visual attention (Romei et al., 2012). Similarly, tACS impacts cognitive and perceptual performance (for a review see Herrmann et al., 2013). Relevant for the above question on factors counteracting noise, tACS targeting the alpha phase was found to improve the detection of auditory signals in noise (Neuling et al., 2012). However, evidence on TMS and tACS in auditory working memory is sparse. A recent study by Vosskuhl et al. (2015) demonstrated that tACS applied in the theta (4–8 Hz) frequency range is able to slow down the individual theta frequency and consequently to increase the individual short-term memory capacity.

The application of brain stimulation can actively increase and decrease the resultant alpha power in a brain region

(Helfrich et al., 2014). That in turn will allow researchers to test the direct, not to say causal impact of alpha power fluctuations in specific brain regions on auditory working memory and help specify the parsimony of the functional inhibition hypothesis.

Altogether, the expansion of the methodological scope towards connectivity analyses and ECoG as well as brain stimulation will provide in-depth evidence about the complex interactions of brain networks of auditory working memory. This would give also further insight on the neural efficiency of managing working memory limitations.

## 6. Conclusions

The present review has summarized recent studies on the role of neural oscillations in auditory working memory. The data reviewed here show that alpha power is a prominent and also sensitive marker of memory load and memory decay in auditory short-term memory. In particular, the impact of acoustic degradation on memory load is clearly captured by alpha power fluctuations. The reverse effect, that is the beneficial effect of factors counteracting acoustic degradation, modulates alpha power to the same degree, reflecting decreased cognitive demands. Source analyses of the different studies showed that the origins of the alpha power effects are diverse (i.e., they include primarily sensory as well as attention-network areas). These functionally variable brain sites raise the question whether alpha power indeed mainly inhibits these areas as implied by the framework of functional inhibition. Further methodological approaches such as connectivity analyses, ECoG, and brain stimulation will be necessary to gather a more nuanced perspective on the inhibitory role of alpha oscillations.

## Open questions

- How critical are domain-general alpha oscillations to memory function? In other words, how much of auditory working memory function can be explained by occipito-parietal alpha enhancement alone? Electrical, pharmacological, or optogenetic regulation of alpha-generating networks during auditory tasks will be key in answering this question.
- In how far do we require auditory adaptations of the extant, mostly vision-based resource models of working memory? A tentative answer is that current working memory models would profit from incorporating more evidence that probe auditory information, which is characterized by its specific reliance on temporal order.
- Does alpha power reflect the same underlying neural process in working memory versus sensory memory? The data reviewed here cast doubt on such a unitary model of alpha, when considering the diverse sources of alpha power effects and the different direction of effects for temporal expectations.

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