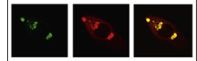


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Review

Attending to auditory memory[☆]Jacqueline F. Zimmermann^{a,b,*}, Morris Moscovitch^{a,b}, Claude Alain^{a,b,c}^aUniversity of Toronto, Department of Psychology, Sidney Smith Hall, 100 St. George Street, Toronto, Ontario, Canada M5S 3G3^bRotman Research Institute, Baycrest Hospital, 3560 Bathurst Street, Toronto, Ontario, Canada M6A 2E1^cInstitute of Medical Sciences, University of Toronto, Toronto, Ontario, Canada

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ABSTRACT

Attention to memory describes the process of attending to memory traces when the object is no longer present. It has been studied primarily for representations of visual stimuli with only few studies examining attention to sound object representations in short-term memory. Here, we review the interplay of attention and auditory memory with an emphasis on 1) attending to auditory memory in the absence of related external stimuli (i.e., reflective attention) and 2) effects of existing memory on guiding attention. Attention to auditory memory is discussed in the context of change deafness, and we argue that failures to detect changes in our auditory environments are most likely the result of a faulty comparison system of incoming and stored information. Also, objects are the primary building blocks of auditory attention, but attention can also be directed to individual features (e.g., pitch). We review short-term and long-term memory guided modulation of attention based on characteristic features, location, and/or semantic properties of auditory objects, and propose that auditory attention to memory pathways emerge after sensory memory. A neural model for auditory attention to memory is developed, which comprises two separate pathways in the parietal cortex, one involved in attention to higher-order features and the other involved in attention to sensory information.

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1. An overview

The way we experience sounds around us does not reflect a purely sensory process, but rather an interaction with higher-order processes such as attention, memory, and expectancies. Past experiences encoded in memory play a large role in shaping auditory perception. For example, deployment of attention to hearing our cellular ringtone in a crowded location will differ based on expectations about receiving a phone call. Irregularities in our auditory environments at home or work will be attended to more strongly than sounds that are commonly encountered. Even infants before they reach six months of age show preference for familiar sounds such as the sound patters that make up their own name (Mandel et al., 1995). The significance of top-down influences on the world we perceive was formulated by Hermann von Helmholtz, an influential thinker and pioneer of modern science, over a century ago. He described perception as emerging from the combination of an external stimulus and judgements we make about the stimulus based on knowledge gained through experience (von Helmholtz, 1867).

In recent years, there has been a surge of interest in studying how attention and memory interact, specifically how attention can be oriented or focused on internal representations (e.g., Chaumon et al., 2009; Patai et al., 2012). So far, the majority of research has focused on understanding this relationship in the visual domain with only few studies dedicated to attention to auditory memory. The studies that do exist are largely separate endeavors not linked together under a larger overarching theme. Yet the topic has a range of real-world implications. Quick and often automatic reactions in emergency situations are largely influenced by familiarity and experience with sound objects, for which semantic relevance is strongly encoded in memory. For example, deployment of attention, arousal, as well as subjective measures of attentional capture in response to hearing emergency alarms are strongly modulated by familiarity with the alarm (Burt et al., 1995; Vaillancourt et al., 2013). Understanding the mechanisms underlying the effects of auditory memory on attentional processes can provide the necessary foundation for developing appropriate health and safety recommendations in real world auditory environments.

The effects of auditory memory on attentional processing can be divided into two separate theoretical domains, which are outlined in this review: 1) attending to auditory memory in the absence of related external stimuli (i.e., “reflective attention”) and 2) the effects of existing memory on guiding/biasing attention. The former portrays our ability to selectively attend to internal representation(s) of auditory features or objects (i.e., attention to memory traces), while the latter describes how memory representations modulate our attentional system. Understanding both perspectives is important for developing a comprehensive theory of attention to memory. For example, both reflective attention and less direct memory-based changes in attention are crucial to everyday communication. Since speech unfolds over time, maintaining and reflectively attending to the signal is necessary to combine individual words into a meaningful discourse. We also retrieve relevant knowledge from long-term memory (LTM) to facilitate both listening and speech comprehension, for instance when orienting towards a familiar voice, or when ignoring information that is deemed irrelevant (e.g., “ums” and “ahs” in speech). Investigating the interplay between attention and memory in audition provides an opportunity to understand how sounds are represented and selected from short-term memory (STM)—a question that auditory scientists have been struggling with for decades.

1.1. Key concepts and aims of the review

Despite the important implications of the topic, how auditory memory influences attention remains a largely neglected field of study within cognitive neuroscience. Our purpose is to review the current literature, and develop a coherent understanding of attention/auditory memory interactions. It is important to first briefly introduce and discuss our conceptualization of auditory attention and auditory memory, since the definitions of these concepts themselves remain highly debated. Numerous models have attempted to understand the precise nature of auditory attention, most commonly defining it as a selective process by which certain sounds in a cluttered auditory environment are filtered out whereas others are not (illustrated by the “cocktail party” example introduced by Cherry, 1953), or in terms of its spatial mechanisms, as a “spotlight” or “filter” which navigates

around an auditory scene (Arnott and Alain, 2002). In the current review, we conceptualize attention as a prioritization of processing to a particular auditory object or feature (e.g., pitch) in our environment or a memory trace of that object/feature. We suggest that while attention is generally focused on sound objects (or memory representations of sound objects), it is also possible to focus on individual features of these representations (Section 2.2.1). Auditory memory is conceptualized as a multi-store system, composed of sensory memory, STM, and LTM, each of which is defined in detail (see Section 2.4 for sensory memory and STM, Section 3.2 for LTM). We propose that information maintained in short-term and long-term stores can be activated to guide attention, though reflective attention to auditory sensory stores may not be possible (see Section 2.3 for further discussion).

To begin, we review evidence from change deafness, to show that attention can be directed to objects in memory to improve detection of changes in our auditory environment, and discuss controversies in the underlying causes of change deafness (i.e., review the role of faulty memory mechanisms in facilitating change deafness). Next, we turn to a discussion of STM and LTM evidence for a modulation of attention. We bring to light several characteristics underlying attention to memory such as the selective limitations of auditory memory and the time-course of memory-guided attentional modulation. Finally, we propose a neural model for attention to auditory memory, and discuss how it interacts with auditory cognition as a whole.

2. Attending to auditory memory representations

Directing attention to STM is often studied experimentally using variants of the delayed-match-to-sample task. In these paradigms, a stimulus array that comprises either one or several items is first presented, and participants are instructed to remember it. Then, the array is removed and participants must maintain its contents in memory. During this retention interval, a cue (dubbed retro-cue) indicates to the participant to what in the stimulus array (which is now being maintained in memory) they should attend. After the delay, participants are presented with a stimulus probe and must determine whether or not the probe matches one of the previously encoded items, that is, whether it was in the originally presented array.

Selectively orienting attention to representations in STM, or information retrieved from long-term stores, has been termed “reflective attention”, since it involves “thinking back to” or “reflecting” on stored information (Chun and Johnson, 2011). The study of auditory reflective attention is effectively introduced through the study of change deafness phenomena, where researchers show that orienting attention to sound objects in memory can attenuate change deafness (Backer and Alain, 2012).

2.1. Evidence from change deafness

The widely studied phenomenon of “change deafness” refers to a failure to notice changes in the auditory environment. In a typical change deafness experiment, participants are presented with two auditory scenes separated by a retention interval. The auditory scenes often consist of complex sounds (e.g., musical sounds, animal sounds) presented simultaneously from different locations. The second scene may contain a switch in location, substitution in object identity, presentation of a novel object, or no change. Individuals required to make same/different responses for the two scenes often demonstrate high error rates, around 30% (Gregg and Samuel, 2008; Vitevitch and Donoso, 2011). Moreover, failure to detect changes often occurs even when the auditory change is large and distinct, such as changing speaker identity (Fenn et al., 2011; Vitevitch, 2003) or when salient and semantically relevant auditory objects (e.g., identifiable animal calls) are added or deleted from sound scenes (Pavani and Turatto, 2008). Although the nature of auditory objects in general has been considerably debated (for a review see Griffiths and Warren, 2004), we will define an auditory object according to its most widely accepted definition—as an acoustic experience or construct that corresponds to a sound which can be attributed to a particular source (Alain and Arnott, 2000; Bizley and Cohen, 2013).

Based on a compilation of studies, Dickerson and Gaston (2014) suggested that similarity (between the changing auditory target and the remaining signal) and uncertainty (difference between the stimulus and expectations about the stimulus) are the primary factors that contribute to change deafness. While the former concerns the characteristics of the stimulus and, therefore, reflects a perceptual process, the latter indicates that top-down online processes play a large role in biasing attention. For example, when auditory targets or the embedding context are altered from the existing schema that are defined in memory (established expectancy), then detection of change increases (Dickerson and Gaston, 2014).

2.2. Attenuating change deafness: attending to representations in auditory short-term memory

Eramudugolla et al. (2005) provides one of the first evidence suggesting that change deafness may be related to attentional limitations. Using a cueing paradigm, they showed that knowing in advance which sound object would change in an auditory scene that comprised more than four objects significantly attenuated change deafness. Along a similar vein, Backer and Alain (2012) showed that change detection can be improved by directing attention to auditory representations in STM. Memory cues presented several seconds after encoding of multiple sound objects served to activate auditory representations and guide attention towards these representations, thus reducing change deafness. By using retro-cues to bias a listener's attention to memory of a sound object (reflective attention), rather than cueing an object prior to the presentation of the stimuli (perceptual attention studied by Eramudugolla et al., 2005), Backer and Alain (2012) provided direct evidence for our ability to orient attention to sound

object representations and use auditory STM to optimize goal-directed behavior. Based on this work, several principles of attention to auditory memory, as compared to attention to visual memory, are discussed below (see also [Backer and Alain, 2014](#)).

First, our ability to retrieve auditory information from STM appears to follow a longer time course than that observed in the visual modality. For instance, a visual retro-cue presented immediately before the probe, or even after probe onset, successfully attenuates change blindness ([Landman et al., 2003](#)) whereas in the auditory modality a retro-cue presented 500 ms before the probe has little effect on change detection ([Backer and Alain, 2012](#)). Therefore, the deployment of attention to auditory memory is not necessarily a quick and automatic process. More time is needed to search through auditory than visual STM and bring forward the task-relevant representation.

Second, despite limitations in the time course of auditory reflective attention, studies have shown that sound object representations in STM are surprisingly long-lasting. Compared to visual change detection studies that indicate that the retro-cue effect may decay quickly (e.g., [Becker et al., 2000](#); [Zhang and Luck, 2009](#)), [Backer and Alain \(2012\)](#) showed that cueing attention to a sound object representation four seconds after stimulus offset improved task performance. Moreover, immediate retro-cues were not necessarily more effective than cues presented several seconds after the offset of the complex auditory scene. Auditory memory traces have been shown to last up to 10 s ([Cowan, 1984](#)), and could potentially bias selective attention, although the limit of this has yet to be determined.

Third, the number of visual stimuli within the array influences how retro-cues are used to benefit attention and performance ([Backer and Alain, 2014](#)). When the size of the array is within the limits of visual STM capacity (around 3–4 items according to [Cowan, 1998](#)), retro-cues are used to prioritize the cued item over the uncued items, but uncued items are still maintained in memory ([Astone et al., 2012](#)). However, when capacity limits are exceeded, uncued items are discarded from memory. That is, there appears to be no benefit of valid cueing relative to neutral (i.e., uncued) trials, and there is a significant cost of invalid cueing. It remains to be determined whether attention to auditory memory is similarly affected by array size, since auditory studies have only tested auditory scenes that comprised three concurrent naturalistic sounds ([Backer and Alain, 2012](#)). Moreover, memory capacity limits for the specific sounds used in a particular paradigm must first be examined. For instance, the capacity of auditory memory may differ depending on the kind and complexity of stimuli used (verbally spoken words vs. complex sounds).

The neural correlates of auditory reflective attention have been investigated with scalp recordings of event-related brain potentials (ERPs). [Backer et al. \(2015\)](#) used a paradigm analogous to that of [Backer and Alain \(2012\)](#) and found an ERP modulation over the left frontal scalp region following the presentation of the retro-cue. In addition, they observed alpha and beta power suppression over midline frontal and posterior scalp regions, which were thought to reflect top-down control of attention. Notably, directing attention

toward spatial and semantic features of auditory objects generated different patterns of neural activity. In their study, participants showed greater improvement in change detection when attention was directed toward the sound object's location (i.e., spatial cues) than when attending to its identity (i.e., semantic cues). This suggests that when complex sounds are presented simultaneously, a sound object representation is more easily accessed via its distinctive location feature than its identity. It is important to note that in [Backer et al. \(2015\)](#), the spatial cue guided the listeners' attention to a specific location, which then involved making a semantic decision (i.e., which semantic category does the object belong to?). Conversely, cueing a sound identity involved making a decision about the actual location of the cued object. Other studies indicate that change deafness depends largely on semantic processing ([Gregg et al., 2014](#); [Gregg and Samuel, 2009](#)). For example, [Gregg and Samuel \(2009\)](#) manipulated either acoustic or semantic similarity of stimuli in a change deafness paradigm and found that participants had more difficulty noticing a change when auditory stimuli were semantically related to the original object, indicating that listeners rely on higher-level properties of the auditory signal rather than low-level physical information.

In general, reflective attention guided by retro-cueing (attending to internal representations of auditory objects) is associated with a distinct pattern of activity from attention activated by cues preceding task-relevant stimuli (i.e., pre-cueing). Moreover reflective visual and auditory attention likely activates similar pre-frontal regions, associated with top-down control ([Buchsbaum et al., 2005](#); [Johnson et al., 2005, 2007](#)). For instance, the middle frontal gyrus, a region within the left dorsolateral prefrontal cortex, was first identified by [Rave et al. \(2002\)](#) as being strongly activated when participants were asked to “think back on” a previously presented word stimulus relative to when asked simply to read a word. Research conducted by [Buchsbaum et al. \(2005\)](#) and [Johnson et al. \(2005\)](#) implicated the left prefrontal cortex in both visual and auditory attention to memory tasks using spoken and written word stimuli. This led [Backer and Alain \(2014\)](#) to theorize that reflectively attended information is supra-modally transformed into articulatory or phonological code that is modulated by regions in the prefrontal cortex. However, it is unclear whether reflective attention in general, only verbal information (i.e., auditorily and verbally presented words), or semantically recognizable and nameable objects are processed by these regions. Further research using non-verbal stimuli and stimuli that are less semantically informative (e.g., tones) might help determine the precise role of the prefrontal cortex in reflective attention.

While visual and auditory reflective attention rely on the same supra-modal prefrontal neural substrates, each is also associated with a distinct activation that reflects where the representation is processed in the first place (however, with lower activation during reflection than perception) ([Backer and Alain, 2014](#); [Backer et al., 2015](#)). For instance, attending to internal representations of spoken words when they are no longer physically present will stimulate regions of the auditory cortex that are also activated when the word is initially heard ([Buchsbaum et al., 2005](#)). Likewise, reflectively

attending to written words will activate the visual cortex similarly as reading them (Johnson et al., 2005).

2.2.1. Attending to memory: object or feature-based processing?

The object versus feature-based debate of auditory attention is central to research on auditory reflective attention. Do we attend to objects as a whole, or rather to specific features of auditory stimuli? Early studies of auditory selective attention suggested that the selection process relied predominantly on representations of task-relevant features, which we refer to as feature-based attention models. However, more recent studies have shown that auditory attention, like visual attention, is focused on an object (Alain and Arnott, 2000; Backer and Alain, 2012; Bressler et al., 2014; Shinn-Cunningham, 2008). Compared to processing in the primary visual cortex however, preprocessing of auditory input into combinations of features may occur earlier along the auditory pathway. For example, King and Nelken (2009) suggested that the primary auditory cortex is located at a higher level of processing than the primary visual cortex, and that its main organizing principle is higher-order to simple feature detection.

A purely feature-based view of auditory attention has been criticized because our ability to attend to specific features of an auditory stimulus (e.g., pitch, location) is often impaired by changes in another irrelevant feature (Dyson and Quinlan, 2004; Mondor et al., 1998), and attending to multiple feature dimensions is costly (Dyson and Quinlan, 2002). However, feature and object-based mechanisms of auditory attention likely coexist (Krumbholz et al., 2007), and it is difficult to resolve the dilemma in a definitive manner because the definition of both auditory objects and auditory features remains largely debated. For instance, some of the most convincing evidence for feature-based attentional processing is found through dichotic listening studies, where listeners attending to one of two simultaneously presented auditory streams (each presented in one ear) display increased activation contralateral to the attended location (Alho et al., 1999; Lipschutz et al., 2002; Tzourio et al., 1997). Yet, since encoding of spatial location involves complex multi-feature calculations, location may not be considered as a genuine “sound feature.” Spatial-based attention is often distinguished from pure feature-based attention based on the salience of location, and because of different neural mechanisms underlying location-based processing (Golomb et al., 2014; Kwak and Egeth, 1992; Lamy and Tsal, 2001; Ling et al., 2009). Overlooking the debate about the true nature of “features,” it should also be noted that the findings of hemispheric contralaterality of responses to mono-aural signals may simply be the result of the asymmetry of excitatory projections from subcortical regions, and are perhaps not valid examples of real feature-based processing (Krumbholz et al., 2007). It is likely that auditory attention acts at different processing levels and through redundant circuits, and that it can be guided by objects, smaller feature clusters (i.e., location), as well as individual low-level features.

In summary, the effects of an informative cue, as opposed to a neutral cue, during a change detection task show that attention can be retrospectively oriented to a sound object

representation in STM. Auditory attention, like visual attention, can be characterized as object-based rather than feature-based, though a sound object representation can be accessed via one of its semantic or location features (Backer et al., 2015; Krumbholz et al., 2007). Notably, these studies provide converging evidence that listeners automatically parse auditory scenes into separate sound objects (a process which is often semantically guided), and can actively shift their attention to a specific object within auditory STM.

2.3. Controversies in change deafness: encoding failure or a failure in comparing incoming stimuli with current memory traces?

Increasing interest in the phenomenon of change deafness has shifted toward understanding whether it reflects a faulty memory, or an inability to compare incoming stimuli with representation(s) in STM. It is well known that only a portion of incoming information is selectively attended due to resource limitations, and that attended objects are better encoded and remembered than unattended ones. Thus, it made sense to attribute change deafness to a failure to encode the undetected changes in the first place. McAnally et al. (2010), however, demonstrated the reverse. Namely, that detection of changes in our auditory environment is strongly affected by capacity to encode and maintain objects in memory (i.e., changes are detected if the changed objects are strongly encoded in memory). In their study, participants were asked to identify changes (disappearance of an object from an initial scene containing four, six or eight items) in complex auditory scenes. They found that successfully detected change trials were accompanied by enhanced encoding of the changing auditory objects (i.e., measured as the rate of correctly identifying which object was deleted), compared to undetected change trials where memory for the changed stimulus was no higher than chance level. These findings are noteworthy because they were based on a trial-by-trial analysis examining whether inability to detect changes in a specific scene was accompanied by poor memory for that stimulus, rather than analyses of aggregate change detection (e.g., Gregg and Samuel, 2008).

Although behavioral studies suggest that faulty sensory encoding may account for some of our inability to detect changes, change deafness occurs even when an initial sensory memory for changed objects is intact (Fenn et al., 2011; Gregg et al., 2014; Gregg and Samuel, 2008; Puschmann et al., 2013). The inability to detect changes even when the changed objects are well encoded has also been found in visual studies of change blindness (Angelone et al., 2003; Mitroff et al., 2004). Recent electrophysiological studies using complex scenes with a number of irrelevant streams have shown that undetected changes are encoded and represented in the auditory cortex (Grimm et al., 2011; Gutschalk et al., 2008; Königs and Gutschalk, 2012; Puschmann et al., 2013), though only at a sensory level. These changes however fail to initiate processing in higher-level brain regions required for conscious change detection, providing evidence that change detection occurs along multiple levels of a seemingly hierarchical auditory pathway (see Puschmann et al., 2013 and Grimm et al., 2011). For example, in the paradigm employed by

Puschmann et al. (2013), participants heard three consecutively presented auditory scenes, each comprised of six auditory streams. They were asked to decide whether the scenes were identical or if the pitch of one stream changed. The electrophysiological results revealed an early change detection process that occurred independently of conscious detection (mid-latency N1 responses 40 ms after change onset) (Grimm et al., 2011; Puschmann et al., 2013; Sonnadara et al., 2006). Only those changes which were successfully detected were associated with MMN responses in the auditory cortex (Puschmann et al., 2013).

It is likely that voluntary attention to auditory memory emerges after sensory memory (see Fig. 1). In contrast to sensory memory which is vulnerable to change by incoming information, objects in STM are more stable and are not subject to overwriting by new incoming acoustic data (Durstewitz et al., 2000). We propose that information maintained in sensory memory may not have the capability to bias attention unless it is transferred to and integrated within more stable STM stores.

The most prevalent account of change deafness attributes change detection failures to a mismatch between the level of representation of incoming and stored information (e.g., Gregg and Samuel, 2008, 2009). Specifically, even if memory representations are robust, they contain a coarse representation of auditory objects compared to perceptual information which is rich in acoustic detail. For example, Gregg and Samuel (2009) showed that auditory representations are composed of abstract information more than physical detail which can lead to difficulties in assessing whether they match with incoming perceptual information.

This perspective is supported by change detection studies showing that modifying the changed target object to be acoustically different from, but semantically related to the original pre-change target, resulted in more errors (i.e., failures to detect change) than when the post-change target was semantically different from the pre-change target. Others have proposed that change deafness also occurs due to informational load, which exceeds attentional resources (Dickerson and Gaston, 2014). Both of these perspectives suggest that even when memory for auditory stimuli is intact, we can fail to utilize these resources to optimize perception in certain circumstances (i.e., when comparing different

levels of representations or when load is too high). Further research is required to determine the extent to which cognitive, attention and memory factors play a role in facilitating change detection and to explain the mechanisms underlying failures to successfully attend to memory representations.

2.4. Attention to sound objects in short-term memory

Attention can be focused on sound object representations in STM, a process which allows us to effectively optimize our auditory experience of the world while conserving limited attentional resources. We propose that top-down and voluntary attention for auditory objects stored in memory does not occur immediately, but likely emerges after sensory memory.

Here, it is important to clarify the distinction between sensory and short-term/working memory. Incoming information is first retained within the high-capacity sensory store for a brief duration, generally thought to last around 10 s (Cowan, 1984; Sams et al., 1993; Winkler and Cowan, 2005). While a large quantity of acoustic detail is absorbed into the sensory store, only a small portion is transferred to the lower-capacity STM, where information is characterized with more abstract representations of the auditory signal. Originally, it was agreed that attention was needed to transfer information to STM (based on Atkinson and Shiffrin's (1968) model of memory), but recently the strict division of sensory and STM by demands on attention has been questioned. Wheeler and Treisman (2002) proposed that attention is required to integrate features of the incoming information stream, but that individual features can be stored in parallel without demand on attention.

The duration of STM has been estimated at about 10–30 s (Cowan, 1984; Jonides et al., 2008). Indeed, though they are commonly conceptualized as separate stores, the distinction between sensory and STM remains fuzzy, as the two are predominantly distinguished by time. It has been proposed that while sensory memory is vulnerable to interference by similar incoming acoustic information, objects stored in STM are less susceptible to be overwritten by irrelevant stimuli (Cowan, 1984; Durstewitz et al., 2000). However, it is important to note that interference effects occur even after objects are “consolidated” in short-term stores (Jonides et al., 2008).

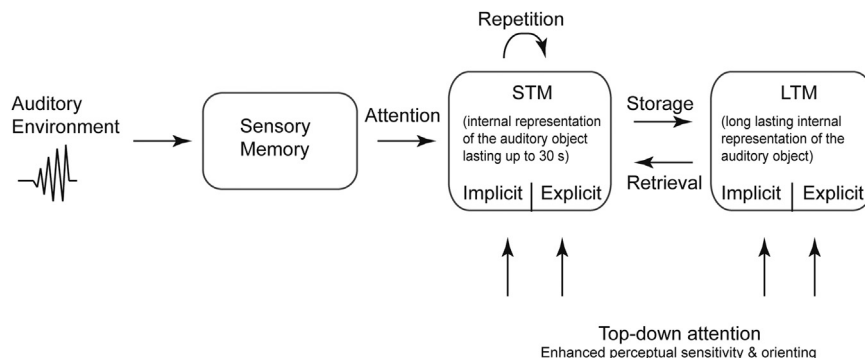


Fig. 1 – Formation of auditory memory and subsequent biasing of attention by internal memory representations (on the basis of Atkinson and Shiffrin's (1968) basic multi-store model of memory). Voluntary attention-to-auditory-memory pathways emerge after sensory memory.

Both sensory (echoic) and STM are critical for encoding and extracting regularities in complex acoustic environments where sound sources are moving or changing frequently. Especially in complex and unpredictable auditory environments (e.g., social settings where the flow of conversation is turbulent), it is often the case that we do not perceive all of the content of one auditory signal. Sensory and STM allow us to mentally play back in time previously occurring sounds to which attention was not explicitly directed, which can occur actively (i.e., active replaying) as well as through passive attention to stored information (i.e., involuntary attention, which is not consciously directed). During speech perception, we often attend to memory representations of the incoming speech signal (e.g., being able to mentally replay what someone just said). Moreover, auditory sensory memory can aid in filling in fragments of the auditory signal (Shinn-Cunningham, 2008), though this does not necessarily involve reflective attention.

According to the well known multi-store model of memory originally proposed by Atkinson and Shiffrin (1968), attention is required to successfully transfer information from sensory stores to STM. Recent work elaborates on the original theory, suggesting that both top-down spatial and central attention is needed to protect sensory information from interference and pass it to STM, where raw sensory features can be bound together to form coherent objects (Landman et al., 2003; Sligte et al., 2010). As mentioned earlier, compared to processing in the primary visual cortex, early auditory processing may be responsible for combining components of the sound signal over frequency and time to create higher-order interpretations of the auditory environment.

Currently, it is proposed that voluntary reflective attention is at work only after the transfer to short-term stores has occurred (Fig. 1). This model is based on discussed research (see Section 2.3.) showing that changes in the auditory environment are often encoded at the sensory level, but are not retained long enough to bias our attentional system (Puschmann et al., 2013). Susceptibility of objects in sensory stores to interference and overwriting by task-irrelevant information (e.g., proactive or retroactive interference) may be a contributing factor. For instance, Visscher et al. (2009) showed strong proactive interference and carryover effects from previous trials in a task where participants were required to make same/different judgments for two successively presented auditory stimuli. Proactive interference was especially salient when the study items were physically similar. Although Visscher et al. (2009) described the effect as interference of STM, the retention intervals used were more characteristic of sensory memory (1 s presentation, with 250 ms ISI).

Here, we should clarify that we are not proposing that sensory activation occurs *before* higher-level processing during reflective attention. When focusing attention on sound objects in memory, higher-level representations of the auditory signal are activated, rather than low-level sensory detail (e.g., Backer and Alain, 2012). For example, when “thinking back on” the familiar sound of your grandmother’s voice (reflective attention to LTM), the attended memory will likely involve a complex and multi-faceted higher-level representation. Further, even with effort it may be impossible to activate the precise components of the signal. In contrast with attention to

auditory memory, research has shown that visual attention can be oriented towards representations in sensory memory. For example, Vandenbroucke et al. (2014) successfully employed retro-cueing towards information in iconic memory (which is the early component of sensory memory, lasting only a few hundred milliseconds) as well as fragile memory (the latter stage of sensory memory which is particularly sensitive to interference from novel displays). Moreover, the benefits of retro-cues compared to neutral cues are quite consistent across object-cue retention intervals, such that gains related to retro-cueing operating on contents of iconic memory (150 ms interval) and visual STM (2040 ms interval) do not differ significantly (Astle et al., 2012). Both early and late visual sensory memory can be accessed explicitly, in a similar manner as working memory, which may facilitate voluntary attention to memory. In contrast, the mechanisms underlying sensory memory in the auditory modality remain unclear, including its conscious accessibility.

3. Modulating attention with existing memory representations

As opposed to attention to memory in the genuine sense, where attention is oriented to active internal representations, a second perspective on the interplay of attention and memory examines how attention is modulated by existing information in short-term or long-term stores. Memory-based modulation of attention is commonly studied using cues presented prior to the task-relevant memory object.

3.1. Information in short-term memory guiding attention

The interaction of attention and STM has been revealed by changes in perceptual sensitivity driven by memory for sound features, such as frequency and timbre. These experiments do not examine attention to memory directly, but rather demonstrate how information already coded in memory is activated and used to facilitate changes in attentional processes. For example, studies have shown that thresholds in detecting and discriminating auditory signals are decreased when individuals know in advance the frequency of the target (Green and McKeown, 2001, 2007; Hubner and Hafter, 1995). In a study conducted by Green and McKeown (2007), the benefit of cueing on signal detection was observed only when cue-signal intervals exceeded 1 s, providing further evidence for the idea that orienting of auditory attention follows a relatively slow time-course.

While auditory cueing may facilitate performance in detecting and discriminating sounds through the monitoring of certain frequency channels (Green and McKeown, 2001, 2007; Hafter et al., 1993), it can also selectively inhibit performance (see Tipper, 1992 for a discussion of attentional inhibition). For example, McKeown and Wellsted (2009) found that discrimination performance (i.e., indicating whether two complex sounds matched or not) declined when previously presented stimuli matched the frequency of a changed target component within one of the incoming sounds. Based on a review of the literature, they posited that the strength or saliency of a given stimulus (assessed in this case via

discrimination performance) arises from the sensory event in combination with the frequency memory trace of recent stimulation (i.e., prime or cue) in frequency-specific channels. Thus, attention plays an important role in the conception of the timbre memory trace; it works to maintain feature strength (i.e., attend to a frequency channel), either through excitatory (attending to a specific frequency channel) or inhibitory (ignoring a frequency channel) mechanisms. This line of studies suggests that memory for recent auditory stimulation shapes, through attention, sensory processing and perceptual sensitivity (see [McKeown and Wellsted, 2009](#)).

On the other hand, it is known that attention is captured by novel, infrequent changes or unexpected events. It remains unclear, however, what is precisely the role of memory in such attentional capture, whether changes in attention are a result of event novelty (e.g., lack of recent memory for the capturing event) or the capturing event's violation of a set of acquired expectations based on memory for a series of events. [Vachon et al. \(2012\)](#) examined this question in an auditory paradigm where participants were given a primary serial recall task, meanwhile listening to a task-irrelevant sequence of voices, which was changed every five trials (e.g., from male to female voice). They found that participants were only distracted from the primary task by the violation of expectations for a specific voice in the irrelevant stream, but attention was not captured when the irrelevant stream was heard for the first time, and therefore novel. Participants also showed a decrease in distractibility by changes in voice as the experiment progressed (e.g., with increasing expectation for the sequence structure). Auditory distraction occurs as a result of violations of learned expectations for hearing a specific stimulus as well as for more global pattern expectations, such as expectation of an increase or decrease of pitch or loudness ([Nostl et al., 2014](#)). Preparatory processes developed through increased familiarity with signal patterns as well as with distracters facilitate greater resistance to distraction as well as enhanced change detection ([Jacobsen et al., 2005](#)). A growing literature has emerged examining auditory predictive modeling, which explains how the auditory system prepares for future events based on expectations and task demands (see [Dalton and Hughes, 2014](#); [Röer et al., 2014](#); [Schroeger, 2010](#)). This field of research provides further support for the importance of expectations encoded in memory, rather than novelty, in driving capture of auditory attention.

3.2. Information in long-term memory guiding attention

In comparison to auditory STM, auditory LTM remains comparably understudied especially for non-verbal material. LTM is considered to differ from STM with regards to duration; typically information held in memory for longer than several minutes falls under LTM. More importantly, LTM is distinguished from STM because information decays slowly from it, and also because LTM does not require direct attending and active maintenance of information through rehearsal strategies ([Jonides et al., 2008](#)). To understand the mechanisms underlying LTM-guided modulation of attention (or make comparisons with visual research), we must first understand the capacities and limitations of auditory LTM.

3.2.1. Auditory long-term memory

In general, research suggests that auditory LTM for non-verbal stimuli is inferior to visual memory ([Cohen et al., 2009](#)), and that while recognition accuracy for example does not differ much between the two modalities over very short durations, auditory memory becomes comparably worse with increasing retention intervals (i.e., intervals over 10 s, see [Bigelow and Poremba, 2012](#)). The limitation of auditory memory does not appear to be a function of restrictions imposed by semantic labeling (i.e., notion that it may be easier to remember visual stimuli because they are often semantically more meaningful), since LTM for recognizable auditory objects and scenes remains deficient compared to visual memory. This is the case even when meaningful labels are provided (e.g., pictures or verbal labels) to increase semantic relevance of auditory scenes ([Snyder and Gregg, 2011](#)).

It is possible that our relatively poor non-verbal auditory memory is the result of having less experience attending to and remembering auditory objects, and therefore having more limited functional neural representations dedicated for their processing. Notably, auditory memory is predominantly verbal in nature ([Snyder and Gregg, 2011](#)), and both STM and LTM for lexical information is superior in the auditory modality. The classic “modality effect” describes this general advantage for remembering acoustically presented verbal information, in free recall (see [Beaman and Morton, 2000](#)), serial recall ([Cowan et al., 2004](#)), short-term sentence recall ([Rummer et al., 2013](#)) and also over long-term retention intervals ([Glenberg, 1984](#)). The modality effect persists under a variety of conditions, and auditory modality advantages have been shown even in memory for novel words ([Bakker et al., 2014](#)). In addition, the advantage for auditorily presented verbal stimuli exists in terms of both implicit memory (i.e., lexicalisation) and explicit memory. The dominance of auditory memory for lexical information over other kinds of auditory objects recommends investigations of auditory memory effects on perceptual and cognitive processes (i.e., memory effects on attention) to focus on verbal stimuli which are well encoded in memory and for which abundant neural representations exist.

3.2.2. Modulating perception and deployment of attention by spatial long-term memory

Perception and goal-directed action appears to be largely influenced by past knowledge and experience with the sounds that surround us. For instance, knowing when our car malfunctions is largely based on prior experience with the usual sounds from the car engine. In a party setting, the familiar voices of a friend or a family member will draw attention more strongly than voices of strangers.

The effects of exposure and familiarity on perception have often been studied using familiar names or voices as target stimuli. The classic subject's own name (SON) effect describes enhanced attention captured in response to hearing one's own name as compared to less familiar names ([Berlad and Pratt, 1995](#); [Carmody and Lewis, 2006](#)). Preferential processing of SON (faster behavioral responding, ERP modulation etc.) is triggered by familiarity as well as strong emotional associations with the stimulus. Moreover, attention capture, enhanced sensitivity and deployment of spatial attention to

well-encoded and highly familiar auditory objects such as our own names appears to be a largely automatic and deeply rooted process, as it has been demonstrated in patients in vegetative and minimally conscious states that have limited capabilities for cognition or awareness (Castro et al., 2014).

Similar familiarity-guided auditory processing has been found with other stimuli that are not necessarily auto-referential, such as music (Soto et al., 2009), cellular ringtones (both personally significant ringtones as well as those trained to become significant; see Roye et al., 2013), as well as known voices (Johnsrude et al., 2013; Newman and Evers, 2007). For example, words spoken by famous voices (Barack Obama, Hillary Clinton) modulate priming effects and enhance sensitivity to changes in the auditory signal (Maibauer et al., 2014). Recently, Johnsrude et al. (2013) showed that voice familiarity not only boosts perception of the familiar object (i.e., enhanced sensitivity to detect the familiar voice among distractors), but can also improve attention for other objects (i.e., effective ignoring of the familiar voice). However, the positive effect of familiarity on voluntary neglect is controversial, as others have found that voice familiarity only has facilitative effects on perception when the familiar voice is the one being attended (Newman and Evers, 2007).

In general, familiar stimuli which are well-encoded in memory have the ability to recruit attentional resources (Soto et al., 2009), and thereby promote enhanced orienting responses and perceptual sensitivity. For instance, thresholds for recognizing a melody embedded in noise or accompanied by other distractors are decreased when individuals know in advance which melody will be played (Bey and McAdams, 2002, 2003; Dowling et al., 1987). These findings are consistent with other research showing schema-driven processing involved in selection and comparison of incoming auditory information with prototypes encoded in LTM (for a perspective on grouping mechanisms in music perception see Deutsch and Dooley, 2013). The positive effects of familiarity on perceptual processing may have strong implications for the treatment of clinical populations (Sarkamo et al., 2013). For example, attenuation of visual neglect using familiar music (Soto et al., 2009), or enhanced orienting responses in patients with traumatic brain injury (Cheng et al., 2013) have been reported.

The majority of studies on memory-guided attention, however, use familiar stimuli (e.g., music, own name etc.) that contain an element of self-relevance in terms of repeated exposure and emotional associations throughout the lifespan, where the LTM is not acquired in a controlled lab setting. There have been some studies on visual attention and LTM that have used learning paradigms to investigate the interplay between attention and LTM in a well controlled lab setting (Summerfield et al., 2006, 2011; Patai et al., 2012). In these studies, participants formed memories for the location of a visual target embedded within scenes (photographs), which facilitated shifts in attention towards remembered target locations after significant retention intervals (e.g., 24 h). Furthermore, there is evidence to suggest that visual memory-guided modulation of spatial attention is facilitated by both explicit (e.g., Summerfield et al., 2011) and implicit (e.g., Ciaramelli et al., 2009) memories. Recently, we developed a new paradigm in which participants created

associations between an audio-clip and a lateralized target tone through repeated exposures. We showed that this laboratory-acquired LTM can bias auditory spatial attention as revealed by faster responses to previously learned than novel target locations (unpublished Zimmermann et al., 2015). As in visual studies, both implicit (i.e., driven by target-context associations which were not remembered/consciously accessible) and explicit memory-guided modulation of attention was found. This study suggests that an existing contextual memory can steer auditory spatial attention, which can in the future be applied to identifying the neural network supporting memory-guided auditory attention.

Overall, the current state of research suggests that robust visual and auditory memories are capable of guiding attention and enhancing perceptual sensitivity even after long retention intervals. We turn towards a more theoretical review of auditory attention to memory, to gain a more comprehensive understanding of its functioning among other aspects of auditory cognition.

4. Developing an auditory attention to memory model

Auditory cognition is mediated by two anatomically and functionally distinct pathways, colloquially known as the “what” and “where” pathways (Alain et al., 2001; Clarke et al., 2000; Maeder et al., 2001; Rauschecker and Tian, 2000, 2003), which originate in the lateral belt of the auditory cortex and have anatomical projections to remote areas in the prefrontal cortex (processing object information) and parietal cortex (spatial analysis functions), respectively (Rauschecker, 2011; Rauschecker and Tian, 2000). While the ventral “what” pathway is dedicated to identifying the incoming auditory signal including semantic and categorical processing, the dorsal auditory pathway is generally associated with localization and orientation towards sound. However, there has been considerable debate about the specific functionality of the dorsal pathway, since it appears to support a wide range of processes, including memory for location of specific sound objects (Alain et al., 2008, 2010; Leung and Alain, 2011) as well as sound characteristics such as movement and loudness (Maeder et al., 2001). It has been implicated in auditory sensory-motor integration, top-down goal driven action (e.g., Warren et al., 2005), as well as lower-level sensory localization processes (e.g., Arnott et al., 2004). This research led us to propose a novel auditory attention to memory model (akin to the visual attention to memory model), which characterizes the dorsal auditory stream as being composed of two dissociated attentional systems in the parietal cortex, one dedicated to top-down modulation of attention (i.e., attention to memory), and a second involved in attention to bottom-up sensory factors (see Ahveninen et al., 2013; Alain et al., 2010; Huang et al., 2012).

The identification of distinct pathways in the parietal cortex for top-down attentional processes (e.g., goal-directed attention) and lower-level sensory input was initially founded in the visual modality (Cabeza et al., 2011; Ciaramelli et al., 2010). The attention to memory (AtoM) model specifies that

the dorsal parietal cortex (DPC) is involved in modulation of attention by retrieval goals and memory processes, and it has been implicated in memory-guided orientation and voluntary goal-related attentional shifts. In contrast, the ventral parietal cortex (VPC) has been tied to response-related attention, and is activated during unexpected attentional capture, for example after invalid memory cueing or in the absence of cues. In vision, the distinction between goal-directed and stimulus-driven attention has been supported by both functional neuroimaging (see [Corbetta and Shulman, 2002](#), for a review) as well as lesion studies ([Berryhill et al., 2007](#); [Berryhill, 2012](#); for review of other models on the role of the parietal cortex in memory, see [Rugg and Vilberg, 2013](#); [Vilberg and Rugg, 2012](#); [Hutchinson et al., 2014](#); [Cabeza et al., 2012](#)).

Similar patterns of functional differences appear in the auditory modality. According to a study conducted by [Alain et al. \(2010\)](#) examining auditory spatial working memory, auditory scene analysis elicits activity in the inferior parietal lobule (within the DPC) related to memory for sound location which is dissociated from response-related activity and activity elicited by unexpected stimuli. Other researchers have classified the distinction as being one of voluntary and more controlled deployment of attention (the network active during memory-guided tasks) versus novelty-driven involuntary attention shifts (e.g., [Huang et al., 2012](#)).

Overall, current research supports an auditory attention to memory model where the role of the dorsal stream is dual, and provides evidence that the parietal cortex plays a crucial role in monitoring and updating location of auditory signals in STM, even in passive conditions when no response is made. However, these studies primarily focus on attention to STM and cue-based modulation over very brief durations. It remains to be determined whether a similar model can also explain findings from studies using LTM tasks.

In addition to top-down and bottom-up modulated attention in the parietal cortex, visual AtoM models also suggest that the two parietal networks are engaged during both memory and perceptual processes. Indeed, several studies have found overlapping activity in the DPC for tasks involving top-down orientation to both memory and perception, and overlapping VPC activity for sensory-guided activity for memory and perception ([Cabeza et al., 2011](#); [Ciaramelli et al., 2010](#); [Sestieri et al., 2009](#)). Nevertheless, others suggest alternative interpretations to account for the found VPC activation (angular gyrus) that was originally associated with memory, namely that it may reflect this region's function as an interface between episodic memory and executive function, rather than memory storage ([Berryhill, 2012](#); [Vilberg and Rugg, 2012](#)). Additional work is needed to examine whether overlapping activation during memory and perception could be found in the proposed auditory attention to memory model.

5. Summary and concluding remarks

In recent years, the more well-studied field of bottom-up influences on attention (i.e., salient stimulus capturing attention) has been joined by endeavors that either directly examine attention to memory representations or assess the impact of an existing or newly created memory in guiding

selective attention (i.e., creating a memory and determining to what extent such knowledge benefits performance).

Clearly, our understanding of attention to auditory memory remains rather limited, and our review is among the first attempts to provide a comprehensive view of these processes. Based on the reviewed publications, several conclusions about the nature of attention to memory for sound objects can be made, which warrant further investigation.

- a) **Voluntary attention to auditory memory emerges after sensory memory; attention is modulated based on short-term and long-term memory stores.**

The attention to memory effect does not emerge immediately, but probably after several seconds of encoding, once the auditory signal is transformed into more abstract representations in STM. Perceptual sensitivity (detection and discrimination) as well as deployment of spatial attention (localization) can be enhanced by auditory STM and LTM, and various characteristics of the auditory signal can be used to modulate perception, including location, physical details (frequency, loudness etc.), and semantic properties of sound. Auditory representations in memory have lasting effects on perception; in some cases the facilitating effect on attention of re-activation of auditory objects is longer than observed in visual attention to memory ([Backer and Alain, 2012](#) as compared to [Becker et al., 2000](#); [Zhang and Luck, 2009](#)).

- b) **Objects are the primary building blocks of attention, though features can also be stored and used to capture attention later.**

The findings point to the importance of semantics in auditory processing. Nevertheless, it is important to note that object and feature-based accounts of auditory attention are not mutually exclusive, and we likely use both to enhance processing to some degree.

- c) **Auditory attention to memory, like all cognitive processes, can be faulty (evidenced by change deafness phenomena), especially when demand on resources is high.**

Failures to detect changes in our auditory environments are likely the result of a host of factors. The most important contributing factor however, appears to be an error in comparing information stored in memory to the incoming signal due to high demand on resources (i.e., load). Just by virtue of their nature as memory representations, the stored information cannot perfectly reflect the raw sensory input. The transformations needed to encode the information (i.e., higher-level nature of the internal representation compared to the detailed and tangible nature of the incoming physical signal) give rise to detection errors.

- d) **We can identify two separate pathways for auditory attention in the parietal cortex, one related to voluntary deployment of attention (i.e., involving top-down mechanisms), and another related to the capture of attention driven by lower-level sensory factors (i.e., bottom-up influences). This classification is similar to one in the visual modality.**

If the auditory attention to memory model can be informed by the more thoroughly studied visual attention to memory system, then we can also hypothesize that the two currently proposed auditory attentional networks may be involved in both perception and memory processing. The top-down network may be active during both perception and memory involving higher-order processing, while the bottom-up network would be active during perception and memory for the auditory signal's physical and sensory details. Further research is needed to investigate this possibility.

Most of the work that does exist in the field stems from investigations of attention to memory in the visual domain. In the future, it will be interesting to develop a better understanding of mechanisms involved in attention to memory which are specific to audition. However, as the two modalities co-exist to inform our everyday experiences, we should also study attention to memory as a more global comprehensive process, for example investigating how visual attention is modulated by auditory memory, or vice versa.

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