

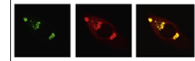


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Review

Neural circuits in auditory and audiovisual memory

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ABSTRACT

Working memory is the ability to employ recently seen or heard stimuli and apply them to changing cognitive context. Although much is known about language processing and visual working memory, the neurobiological basis of auditory working memory is less clear. Historically, part of the problem has been the difficulty in obtaining a robust animal model to study auditory short-term memory. In recent years there has been neurophysiological and lesion studies indicating a cortical network involving both temporal and frontal cortices. Studies specifically targeting the role of the prefrontal cortex (PFC) in auditory working memory have suggested that dorsal and ventral prefrontal regions perform different roles during the processing of auditory mnemonic information, with the dorsolateral PFC performing similar functions for both auditory and visual working memory. In contrast, the ventrolateral PFC (VLPFC), which contains cells that respond robustly to auditory stimuli and that process both face and vocal stimuli may be an essential locus for both auditory and audiovisual working memory. These findings suggest a critical role for the VLPFC in the processing, integrating, and retaining of communication information.

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Q3 1. Introduction

We frequently rely on auditory working memory, for example, when we hear a phone number, and after a brief pause, successfully recall the number to place the call. We also depend on working memory when our train of thought is interrupted and we effortlessly return to it. Although there is much known about auditory pathways and processing, the underlying neural substrates of auditory working memory are poorly understood. Importantly, we do know that damage to sites within frontal, temporal, and parietal cortices can lead to auditory aphasias and memory deficits (Alain et al., 1998; Goerlich et al., 1995; Goll et al., 2010a; Goll et al., 2010b). Additionally, natural aging, strokes, traumatic brain injury and disease can damage the frontal cortex and impair auditory short-term memory capabilities, which can affect daily life. For example, patients with damage to the ventral frontal cortex suffer from language impairments, problems with auditory comprehension, and difficulties with understanding sentences with complex syntax. These are all functions that rely on auditory working memory (Kummerer et al., 2013; Szczepanski and Knight, 2014). Thus, it is imperative to delineate the neural networks and processes that contribute to auditory working memory.

Working memory is defined in multiple ways. One classic definition describes working memory as a method to control attention through the 'central executive', composed of the visuospatial sketchpad, phonological loop, and 'episodic buffer' (Baddeley and Hitch, 1974; Baddeley, 2000). These are broad aspects of cognition and assist with decision making, language processing, and reasoning (Duncan, 2010; Friederici and Gierhan, 2013; Miller, 2013). However, for this review we will use another common definition of working memory which is "to hold an item of information 'in-mind' for a short period of time and to update information from moment to moment" (Goldman-Rakic, 1996).

It has been suggested that nonhuman primates (NHPs) do not have auditory working memory (Scott et al., 2012; Scott et al., 2013), but possess a much more limited short-term mnemonic ability termed 'passive short-term memory'. Previous research argues against this point of view. Although NHP's auditory memory abilities may be less than their capacities for remembering visual information they have demonstrated the ability to discriminate and remember auditory sounds over several seconds (Plakke et al., 2013), which is, by definition, auditory working memory. Evidence for intermediate to long-term auditory memory comes from the established ability of primates to recognize vocalizations of kin (Rendall et al., 1996) and to respond to conspecific and other primate species alarm calls (Zuberbuhler, 2000). In the natural environment, various primate species are able to utilize syntax-like rules when listening to a complex series of call types and alter their behavior accordingly (Arnold and Zuberbuhler, 2008; Lemasson et al., 2010; Zuberbuhler, 2002). For example, if a Campbell's monkey makes an alarm call for an eagle, Diana monkeys will also produce alarm calls signaling eagles; however, if a boom vocalization occurs before the alarm call of the Campbell monkey the Diana monkeys ignores the warning (Zuberbuhler, 2002). The boom

vocalization changes the meaning of the subsequent alarm call, and the Diana monkeys recognize this context and do not send out their own alarm calls. Monkeys housed in a laboratory can also recognize the vocalizations of monkeys from their shared housing room (Adachi and Hampton, 2011; Habbershon et al., 2013). The ability to recognize meaningful vocalizations and alter behavior indicates that primates have some form of auditory memory, perhaps even long-term auditory memory for specific callers, and this leaves the door open for the manipulation of auditory information during working memory as well. The various forms of auditory memory (working, short-term, long-term) and the precise neuronal circuits that each form of memory relies on, is still under investigation. For purposes of this review, the ability to recognize matching or nonmatching auditory stimuli, over a period of several seconds, will be considered auditory working memory.

2. Auditory short-term memory in non-human primates and humans

One reason the mechanisms of auditory memory have not been studied extensively is that it has been difficult to train non-human primates to perform auditory working memory tasks that are similar to those used in the study of visual memory. Nonetheless, there have been some auditory discrimination/memory paradigms used to study the performance of a wide array of species including dogs, dolphins, starlings and non-human primates (Colombo et al., 1990; D'Amato and Salmon, 1984; Fritz et al., 2005; Herman and Gordon, 1974; Kowalska et al., 2001; Wright, 1999; Zokoll et al., 2008). It typically takes longer to train NHPs to learn an auditory discrimination or memory task than to learn a similar task using visual stimuli (D'Amato and Salmon, 1984; Fritz et al., 2005; Hashiya and Kojima, 2001). Wright was successful in training NHPs to learn and remember lists of auditory stimuli (Wright, 1999) which led to great insights demonstrating that auditory memory differed from visual memory in capacity. He showed that monkeys could not remember as many auditory items as visual items. Comparisons of auditory and visual memory curves highlight the notion that auditory memory is more susceptible to interference and less robust compared to visual memory (Wright, 2007). Another study by Fritz and colleagues demonstrated how much harder it was for NHPs to remember acoustic information over short intervals than visual information using the same paradigm (Fritz et al., 2005).

Interestingly, the limited capacity to store auditory stimuli over short temporal intervals is not limited to macaques (Bigelow and Poremba, 2014a). In fact, studies of typical human subjects have demonstrated steeper forgetting curves for auditory stimuli compared to visual stimuli (Bigelow and Poremba, 2014a; Cohen et al., 2009a; Cohen et al., 2011). This finding is similar to the forgetting curves in nonhuman primates (Fig. 1), (Colombo and D'Amato, 1986; Fritz et al., 2005; Hashiya and Kojima, 2001); although, for an exception to the rule, see Visscher et al. (2007). A study examining recognition found that human subjects were significantly worse at recognizing recently heard sounds compared to

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