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Review

Role of attention in the generation and modulation of tinnitus☆

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ABSTRACT

Neural mechanisms that detect changes in the auditory environment appear to rely on processes that predict sensory state. Here we propose that in tinnitus there is a disparity between what the brain predicts it should be hearing (this prediction based on aberrant neural activity occurring in cortical frequency regions affected by hearing loss and underlying the tinnitus percept) and the acoustic information that is delivered to the brain by the damaged cochlea. The disparity between the predicted and delivered inputs activates a system for auditory attention that facilitates through subcortical neuromodulatory systems neuroplastic changes that contribute to the generation of tinnitus. We review behavioral and functional brain imaging evidence for persisting auditory attention in tinnitus and present a qualitative model for how attention operates in normal hearing and may be triggered in tinnitus accompanied by hearing loss. The viewpoint has implications for the role of cochlear pathology in tinnitus, for neural plasticity and the contribution of forebrain neuromodulatory systems in tinnitus, and for tinnitus management and treatment.

Contents

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1. Introduction

Individuals experiencing a persistent tinnitus (chronic ringing of the ears) commonly report that their awareness of tinnitus decreases when they focus on activities that are absorbing and do not require processing of signals in the auditory domain. Modulation of tinnitus awareness can fluctuate rapidly, suggesting either that the neural activity underlying tinnitus is dynamically altered or that its access to consciousness is gated by brain mechanisms that are sensitive to context or task demands. Brain mechanisms that direct the focus of consciousness are commonly described as those that perform top-down attention-like functions. In contrast, studies of neural plasticity in the auditory cortex (Fritz et al., 2003; Weinberger, 2007) and other sensory systems (Ramanathan et al., 2009) indicate that cholinergic neuromodulators deployed to the cortex from the basal forebrain gate synaptic plasticity for unexpected and behaviorally relevant stimuli, performing a bottom-up attention-like function. Attention has been cited as a factor contributing to the development and/or modulation of tinnitus by several models of this condition (Jastreboff, 1995; Jastreboff and Jastreboff, 2006; Zenner et al., 2006; Searchfield et al., 2012b) and as a possible factor contributing to the findings of research studies (Gu et al., 2010; Husain et al., 2011; Hoare et al., 2012). However, the mechanisms by which attention is called and how its role is expressed in the neural changes underlying tinnitus remain a topic of discussion (Roberts et al., 2010).

In this paper we discuss how attention may be involved in the generation of tinnitus and its modulation by task demands. A qualitative model for a role of attention in tinnitus is presented and recent evidence is discussed in the light of it. A key assumption of the model is that in tinnitus there is a disparity between what the brain predicts it should be hearing (this expectation influenced by neural activity underlying the tinnitus percept) and the acoustic information that is delivered by the ear to the brain, when cochlear damage indexed by the audiogram or more sensitive measures is present. The disparity between the predicted and obtained inputs activates mechanisms of auditory attention that may contribute to the establishment and persistence of tinnitus and to its modulation by competing tasks.

2. Neural mechanisms for attention

Understanding how attention might be involved in tinnitus is assisted by a provisional understanding of how attention systems are organized in the normal hearing mammalian brain. Brain regions that show differential activity between a condition in which sounds are attended to, and a condition in which they are not, can be variable depending on the sound attribute to be detected, the prevailing multisensory context, and the significance of the sound including its predictive value and the mental or behavioral operations to be performed (Fritz et al., 2007). This variability arises in part because auditory attention does not operate in isolation of brain networks for other functions that may be engaged by a task, such as comparing task stimuli to those in memory, organizing behavioral responses, and processing feedback from them. The question of how brain networks concerned with auditory attention relate to networks that perform such functions or to those that underlie conscious executive control processes is the topic of extensive ongoing research (Palva and Palva, 2012; Sadaghiani et al., 2009; Dehaene and Changeux, 2011). Also debated are the neural and synaptic mechanisms by which the effects of attention are achieved. Detailed discussions of these topics are found in recent reviews (Fritz et al., 2007; Palva and Palva, 2012; Dehaene and Changeux, 2011) which have provided a backdrop for the discussion to follow. It may be that one should speak not of a single mechanism for attention, auditory or otherwise, but of multiple such mechanisms depending on the sensory modality and stimulus attributes to be attended to and the conditions of testing. Alternatively, top-down and bottom-up forms of attention may share neural resources sufficient to speak of a single system for attention, even though its expression in brain network activity may depend on the specific task stimuli that are present and the behavioral and cognitive performance requirements of the task procedure.

2.1. Top-down and bottom-up auditory attention

Notwithstanding this question, there is a consensus that several brain structures are active in auditory attention in the normal hearing brain, and that auditory attention can be called by bottom-up as well as by top-down signals. Effects attributable to top-down auditory attention are revealed by tasks that direct the focus of attentive processing to auditory signals when bottom-up sensory input and other task variables are held constant. Contrasts comparing brain activations between a silent baseline condition and a condition in which sounds are presented passively have found increased blood oxygen level dependent (BOLD) responses in primary (A1, posteromedial Heschl's gyrus) and nonprimary (A2, surrounding auditory belt and parabelt cortex) auditory regions that reflect stimulus driven activity occurring in these regions (Hall et al., 2000; Johnson and Zatorre, 2005; Petkov et al., 2004; Tzourio et al., 1997), although the possibility of some degree of attention being drawn to the sounds cannot be excluded. When the same sounds are explicitly processed in attention to fulfill a task requirement, brain activity increases further in these auditory regions (Grady et al., 1997; Degerman et al., 2006; Paltoglou et al., 2009), although the pattern of auditory activation may depend on the nature of sounds that are attended. For example, attention to simple spoken syllables (Jäncke et al., 1999) or amplitude modulated pure tones (Gander et al., 2010a,b) has been reported to activate A1 and A2, whereas attention directed to melodies activated posterior regions of the superior temporal gyrus (STG) where more complex forms of auditory processing are believed to take place (Johnson and Zatorre, 2005, 2006; Petkov et al., 2004). Supporting evidence for the view that these activations serve an attentional role is found in the observation that baseline BOLD activity in these auditory regions is elevated when subjects listen in silence for an impending sound (Voisin et al., 2006) and when subjects consciously detect a target noise burst on a discrimination task (hits) compared to trials on which the same sound is not detected (misses; Sadaghiani et al., 2009). In the latter study the anticipatory BOLD increment was larger for hits than misses suggesting that neurons coding for the target sound had been sensitized by attention, although a contribution from behavioral response preparation cannot be ruled out. Interestingly, in the latter study neural activity in two non-auditory brain networks, one consisting of brain regions functionally connected in baseline resting states (the frontal/parietal "default mode" network; Raichle et al., 2001; Raichle, 2010) and the other of non-auditory brain regions functionally coupled during the maintenance of task set (the "intrinsic alertness network" including the anterior cingulate gyrus and anterior insula; Dosenbach et al., 2006, 2007), was also elevated prior to target detection, while activity in a third network (the dorsal attention system, consisting of the right infraparietal cortex and frontal eye fields; Corbetta and Shulman, 2002) was suppressed. Modulation of these additional networks may reflect the discriminative requirements of the detection task and the need to link behavioral responses with specific auditory signals. Overall the results support the view that distinct auditory areas (A1 and A2) are engaged by the specific stimulus content of sounds when top-down auditory attention is called, but that other brain regions can also be modulated. The dorsal attention system associated with vision is activated by sounds that have a spatial