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Review

An integrative model of auditory phantom perception: Tinnitus as a unified percept of interacting separable subnetworks

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ABSTRACT

Tinnitus is a considered to be an auditory phantom phenomenon, a persistent conscious percept of a salient memory trace, externally attributed, in the absence of a sound source. It is perceived as a phenomenological unified coherent percept, binding multiple separable clinical characteristics, such as its loudness, the sidedness, the type (pure tone, noise), the associated distress and so on. A theoretical pathophysiological framework capable of explaining all these aspects in one model is highly needed. The model must incorporate both the deafferentation based neurophysiological models and the dysfunctional noise canceling model, and propose a 'tinnitus core' subnetwork. The tinnitus core can be defined as the minimal set of brain areas that needs to be jointly activated (=subnetwork) for tinnitus to be consciously perceived, devoid of its affective components. The brain areas involved in the other separable characteristics of tinnitus can be retrieved by studies on spontaneous resting state magnetic and electrical activity in people with tinnitus, evaluated for the specific aspect investigated and controlled for other factors. By combining these functional imaging studies with neuromodulation techniques some of the correlations are turned into causal relationships. Thereof, a heuristic pathophysiological framework is constructed, integrating the tinnitus perceptual core with the other tinnitus related aspects. This phenomenological unified percept of tinnitus can be considered an emergent property of multiple, parallel, dynamically changing and partially overlapping subnetworks, each with a specific spontaneous oscillatory pattern and functional connectivity signature. Communication between these different subnetworks is proposed to occur at hubs, brain areas that are involved in multiple subnetworks simultaneously. These hubs can take part in each separable subnetwork at different frequencies. Communication between the subnetworks is proposed to occur at discrete oscillatory frequencies. As such, the brain uses multiple nonspecific networks in parallel, each with their own oscillatory signature, that adapt to the context to construct a unified percept possibly by synchronized activation integrated at hubs at discrete oscillatory frequencies.

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1. Introduction

Tinnitus is commonly defined as the perception of a sound in the absence of an external sound source. Perception is different from sensation. Whereas sensation can be defined as the detection and processing of sensory information, perception is the act of interpreting and organizing this sensory information to produce a meaningful experience of the world and of oneself (De Ridder et al., 2011a; Freeman, 1999). Auditory cortex activation evoked by an acoustic stimulus does not necessarily produce conscious auditory perception (Colder and Tanenbaum, 1999) and auditory perception is possible in the absence of auditory input: more than 80% of people with normal hearing perceive phantom sounds when placed in a soundproof room (Del Bo et al., 2008). Furthermore, some percepts do not reach the level of consciousness. Thus, in non-conscious perception or perception without awareness, the meaning of a stimulus is extracted while the subject cannot consciously identify it or even detect its presence (Dehaene et al., 1998). In addition, deafferentation of auditory input can result in an auditory phantom phenomenon called tinnitus. It is important to understand that some forms of auditory deafferentation are not discovered by behavioral measures such as audiometry (Weisz et al., 2006). Indeed, partial cochlear nerve sections can be performed without detectable changes in hearing thresholds (Dandy, 1941; Schuknecht and Woellner, 1953). This could explain why tinnitus can also occur in the absence of audiometrical hearing loss (Barnea et al., 1990; Lee et al., 2007; Weisz et al., 2006), as this does not preclude auditory deafferentation.

Whereas some people just perceive the phantom sound without being bothered, others suffer emotionally severely from their tinnitus (Axelsson and Ringdahl, 1989), with or without associated cognitive deficits (Hallam et al., 2004). Thus the unified tinnitus percept includes not just a sound percept but also affective components intimately linked to the sound percept.

Tinnitus is a symptom of high prevalence: 10 to 15% of the population in Europe and the USA have prolonged tinnitus requiring medical evaluation (Axelsson and Ringdahl, 1989; Hoffman and Reed, 2004). The prevalence increases with age (Axelsson and Ringdahl, 1989; Hoffman and Reed, 2004) and in noise-exposure, whether occupational (Axelsson and Prasher, 2000; Phoon et al., 1993) or leisure induced (Axelsson and Prasher, 2000; Gilles et al., 2012).

Tinnitus can be subdivided in two entirely different entities, one type in which an internal sound source can be objectivized by an external observer, also known as objective tinnitus, and one in which no perceivable sound source is present, also known as subjective tinnitus (Moller, 2000). Subjective tinnitus is commonly considered to represent an auditory phantom phenomenon (De Ridder et al., 2011a; Jastreboff, 1990). Other classifications describe pulsatile, non-pulsatile and pseudopulsatile tinnitus (De Ridder, 2011). Subjective non-pulsatile tinnitus is the scope of this review. Tinnitus can possibly be caused by different pathophysiological mechanisms (De Ridder et al., 2012c) and it can present itself in multiple forms. The tinnitus type can be different, it can be perceived as a pure tone, a noise-like percept, or polyphonic sound or a combination of these types, with different brain areas involved in the different percepts (Vanneste et al., 2010d), or hypothetically different pathways (De Ridder et al., 2007c). The tinnitus can be perceived unilaterally, bilaterally or holocranially. In bilateral tinnitus it can be perceived as one sound, or it can be perceived as two different sounds in the two ears, all likely to be associated with a different pathophysiology (De Ridder et al., 2007b; De Ridder et al., 2012b) and involving different brain areas (Vanneste et al., 2011a; Vanneste et al., 2011d). There are gender differences in the emotional aspects of tinnitus: in men and women with the same tinnitus intensity, the same tinnitus type and the same amount of distress, there are still differences in mood associated with differences in brain activation (Vanneste et al., 2012a). But most importantly tinnitus can be perceived as a sound with or without distress, with different brain areas involved in tinnitus distress (De Ridder et al., 2011c; Langguth et al., 2012; Schlee et al., 2009b; Schlee et al., 2008; van der Loo et al., 2011; Vanneste et al., 2010a; Weisz et al., 2011; Weisz et al., 2005a; Weisz et al., 2004; Weisz et al., 2005b).

2. Integrating different existing tinnitus models

The first conceptual tinnitus model that was proposed the neurophysiological model, considered tinnitus as an auditory phantom percept (Jastreboff, 1990). It explained the process by which tinnitus emerges, and divided it into three stages; (i) generation; (ii) detection, and (iii) perception and evaluation (Jastreboff, 1990; Jastreboff and Hazell, 1993). The generation could be attributed to many different causes, such as (1) discordant damage of outer (OHC) and inner (IHC) hair cell systems; (2) crosstalk between the VIII nerve fibers; (3) ionic imbalance in the cochlea; (4) dysfunction of cochlear neurotransmitter systems; (5) heterogeneous activation of the efferent system; (6) heterogeneous activation of Type I and II cochlear afferents. The detection was proposed to be based on a pattern recognition principle of decoding auditory information by neural network mechanisms (Jastreboff, 1990; Jastreboff and Hazell, 1993).The perception and evaluation process was proposed to involve different cortical as well as memory and limbic areas. (Jastreboff, 1990; Jastreboff and Hazell, 1993). The model suggests that the abnormal neural activity that causes tinnitus will be typically generated at the periphery of the auditory system, possibly in the dorsal cochlear nucleus (Jastreboff and Hazell, 2004; Kaltenbach, 2006) (see Fig. 1). This signal may then be detected and further processed in the subconscious part of the brain. Finally, it reaches the high cortical levels of the auditory system where it can