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Review

Function and plasticity of the medial olivocochlear system in musicians: A review

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A B S T R A C T

The outer hair cells of the organ of Corti are the target of abundant efferent projections from the olivocochlear system. This peripheral efferent auditory subsystem is currently thought to be modulated by central activity via corticofugal descending auditory system, and to modulate active cochlear micromechanics. Although the function of this efferent subsystem remains unclear, physiological, psychophysical, and modeling data suggest that it may be involved in ear protection against noise damage and auditory perception, especially in the presence of background noise. Moreover, there is mounting evidence that its activity is modulated by auditory and visual attention. A commonly used approach to measure olivocochlear activity noninvasively in humans relies on the suppression of otoacoustic emissions by contralateral noise. Previous studies have found substantial interindividual variability in this effect, and statistical differences have been observed between professional musicians and non-musicians, with stronger bilateral suppression effects in the former. In this paper, we review these studies and discuss various possible interpretations for these findings, including experience-dependent neuroplasticity. We ask whether differences in olivocochlear function between musicians and non-musicians reflect differences in peripheral auditory function or in more central factors, such as top–down attentional modulation.

This article is part of a Special Issue entitled "Music: A window into the hearing brain".

1. Introduction

Musicians – most notably professional musicians – often show exceptional auditory abilities, especially, in perceptual tasks involving pitch discrimination (Kishon-Rabin et al., 2001; Micheyl et al., 2006), auditory memory (Boh et al., 2011; Parbery-Clark et al., 2011; Strait et al., 2012), or auditory attention (Strait et al., 2010, 2013a). The neural basis of enhanced auditory perceptual performance in musicians compared to non-musicians is not entirely clear. Several studies have suggested that early musical training can interact with the development, maturation, and plasticity of the central auditory system (Ellis et al., 2012; Herholz and Zatorre, 2012; Hyde et al., 2009; Oechslin et al., 2013; Strait et al., 2013b). However, much less is known concerning the influence of musical training on peripheral auditory function. Interestingly, experimental findings obtained during the last twenty years or so suggest that the activity of the medial olivocochlear system (MOCS) – an efferent neural pathway originating in the brainstem, which projects directly onto the cochleas – is enhanced in musicians (Brashears et al., 2003; Micheyl et al., 1995a, 1997a; Perrot et al., 1999). These findings may have important implications for our understanding of the neural basis of music-related changes in auditory function and processing. On the peripheral side, since the MOCS modulates active cochlear micromechanics (ACMs), which are involved in fine auditory sensitivity, improved frequency selectivity and enhanced dynamic range, an increase in MOCS activity may facilitate auditory perception, notably in competitive musical environments. On the central side, since the MOCS is likely to be under a top–down control of corticofugal descending auditory system (CDAS), a stronger MOCS may be interpreted as reflecting a strengthening of corticofugal modulation, thereby open to attentional modulation and training-induced plasticity.

In this article, we provide an overview of the main research findings concerning MOCS function in musicians. We then consider

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Abbreviations

ACMs	active cochlear micromechanics
AN	auditory nerve
BBN	broadband noise
BM	basilar membrane
CDAS	corticofugal descending auditory system
CN	cochlear nucleus
dB	decibels
DPOAE(s)	distortion-product otoacoustic emission(s)
EOAE(s)	evoked otoacoustic emission(s)
IDL	intensity difference limen
IHC(s)	inner hair cell(s)
IN	interneurons
(k)Hz	(kilo)hertz
LE	left ear
MEM(R)	middle-ear muscle (reflex)
MOC(S)	medial olivocochlear (system)
ms	milliseconds
Mus	musicians
Nmus	non-musicians
OAE(s)	otoacoustic emission(s)
OHC(s)	outer hair cell(s)
RE	right ear
SEA	stimulus-equivalent attenuation
SFOAE(s)	stimulus-frequency otoacoustic emission(s)
SL	sensation level
SOAE(s)	spontaneous otoacoustic emission(s)
SOC	superior olivary complex
SPL	sound pressure level
TDT	tone decay test
TEOAE(s)	transiently-evoked otoacoustic emission(s)

physiological mechanisms that may be responsible for experience-dependent changes in MOCS function. In particular, we discuss central and peripheral neuroplasticity hypotheses, as well as the functional, perceptual, and cognitive consequences of MOC activity enhancement on peripheral auditory function and central auditory processing. To put the review into context, we start with a brief description of the main anatomical and physiological characteristics of the MOCS (for detailed reviews, see Guinan, 2006, 2011; Robles and Delano, 2008).

2. Overview of anatomical and physiological characteristics of medial olivocochlear system

2.1. Organization of human olivocochlear system

The olivocochlear bundle, also known as the auditory efferent system, was initially described in the cat by Rasmussen (Rasmussen, 1946). As the name indicates, this system originates in the superior olivary complex (SOC), which is located in the ventral part of the pons, and it projects bilaterally onto the cochleas via the vestibular nerves. It involves two subsystems with distinct anatomical and functional features: the lateral olivocochlear system, and the medial olivocochlear (MOC) system (Warr and Guinan, 1979). Although current knowledge concerning the anatomy of these subsystems stems primarily from experimental data in feline and rodent animal models, post-mortem studies in humans and comparative studies in non-human primates indicate a similar subdivision of the human olivocochlear system in those species (Hilbig et al., 2009; Moore, 2000). To our knowledge, the function of lateral olivocochlear system has never been assessed in humans; accordingly, in this review, we focus on the MOCS.

2.1.1. The medial olivocochlear system

The MOCS originates in the medial part of the SOC which, in humans, corresponds to nuclei of the periolivary region. It is comprised of thick myelinated nerve fibers which project predominantly onto the contralateral cochlea through the crossed olivocochlear bundle. Other fibers project onto the ipsilateral cochlea, through the uncrossed (or direct) olivocochlear bundle. Both types of MOC fibers form synapses with outer hair cells (OHCs).

2.1.2. Interspecies differences in mammalian olivocochlear system

Two main differences in the anatomy of the olivocochlear system between humans and other mammals have been reported. Firstly, in humans, at least one half to two thirds of olivocochlear fibers are MOC fibers (Moore, 2000). Secondly, comparative studies with monkeys suggest that the number of crossed fibers in humans is slightly higher than, or equal to, the number of uncrossed fibers (Guinan, 2006; Hilbig et al., 2009).

2.2. Physiology of medial olivocochlear system

2.2.1. Neurophysiological properties of olivocochlear fibers

Most electrophysiological studies have focused on MOC fibers in small mammals (Robertson and Gummer, 1985; Warren and Liberman, 1989). However, the main findings of these studies have been replicated in humans (Berlin et al., 1995; Chabert et al., 2002; Veuillet et al., 1991). One important physiological property of olivocochlear fibers is that they are responsive to many kinds of acoustic stimulations – e.g., tones, broadband noise or amplitude-modulated tones – applied ipsilaterally, contralaterally or bilaterally. This property is the basis of the non-invasive functional assessment of MOC system activity through the acoustic suppression of otoacoustic emissions (OAEs) (Collet et al., 1990; see Section 2.4). Moreover, olivocochlear spontaneous activity coupled with cochlear effects of transection of the olivocochlear bundle suggest that the MOCS may exert a basal tonic control of the cochlea (Bonfils et al., 1987; Zheng et al., 2000b; see also Subsection 4.1.2).

2.2.2. Medial olivocochlear acoustic reflex

Olivocochlear fibers constitute the efferent pathway of an acoustic reflex loop (Liberman and Guinan, 1998). Two kinds of MOC acoustic reflexes are described: ipsilateral and contralateral (see Fig. 1). The ipsilateral reflex – which mobilizes both crossed afferent and efferent fibers – involves the contralateral crossed MOC bundle, whereas the contralateral reflex – consisting of a single afferent crossing – involves the ipsilateral uncrossed MOC bundle (Guinan, 2006).

2.2.3. Olivocochlear effects on peripheral auditory system

The main neurotransmitter of MOC fibers is acetylcholine. Its synaptic release induces hyperpolarization of OHCs, resulting in direct or indirect inhibition of OHC motilities[1] (see Subsection 2.4.1; for a review on cellular and molecular mechanisms of OHC efferent modulation, see Russell and Lukashkin, 2008; Wersinger and Fuchs, 2011). The main consequences of MOCS activation on cochlear

[1] For simplicity, in this article, the expression “OHC motilities” is used to refer both to somatic electromotility and to active hair-bundle motility.

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