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Olivocochlear efferents: Their action, effects, measurement and uses, and the impact of the new conception of cochlear mechanical responses

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ABSTRACT

The anatomy and physiology of olivocochlear (OC) efferents are reviewed. To help interpret these, recent advances in cochlear mechanics are also reviewed. Lateral OC (LOC) efferents innervate primary auditory-nerve (AN) fiber dendrites. The most important LOC function may be to reduce auditory neuropathy. Medial OC (MOC) efferents innervate the outer hair cells (OHCs) and act to turn down the gain of cochlear amplification. Cochlear amplification had been thought to act only through basilar membrane (BM) motion, but recent reports show that motion near the reticular lamina (RL) is amplified more than BM motion, and that RL-motion amplification extends to several octaves below the local characteristic frequency. Data on efferent effects on AN-fiber responses, otoacoustic emissions (OAEs) and human psychophysics are reviewed and reinterpreted in the light of the new cochlear-mechanical data. The possible origin of OAEs in RL motion is considered. MOC-effect measuring methods and MOC-induced changes in human responses are also reviewed, including that ipsilateral and contralateral sound can produce MOC effects with different patterns across frequency. MOC efferents help to reduce damage due to acoustic trauma. Many, but not all, reports show that subjects with stronger contralaterally-evoked MOC effects have better ability to detect signals (e.g. speech) in noise, and that MOC effects can be modulated by attention.

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1. Introduction

The olivocochlear (OC) efferents are part of brainstem-to-cochlea reflex pathways that allow stimulus-related control of the cochlea, and provide a way for the central nervous system to affect hearing at the most peripheral neural level. There have been many reviews of OC efferents (e.g. Guinan, 1996, 2006, 2010; 2011, 2012). Here we concentrate on new efferent work, new interpretations based on recent cochlear-mechanical data, controversial issues, and areas that need more study. We briefly review basic, long-established efferent anatomy and physiology. Since space is limited, for citations to older literature we refer readers to the reviews listed above, and for recent work we do not cite all relevant references.

2. Efferent anatomy and action in the cochlea

2.1. Efferent anatomy

Olivocochlear (OC) neurons receive sound-driven inputs from the cochlear nucleus and form brainstem-level acoustic reflexes. OC neurons receive descending inputs that allow higher neural centers to modulate the OC reflexes. In almost all mammals there are two groups of olivocochlear efferents: medial OC (MOC) and lateral OC (LOC) efferents.

MOC neurons are located in the superior olivary complex medial, ventral and extending slightly anterior to the medial superior olivary nucleus. They have myelinated axons that synapse on outer hair cells (OHCs). In most experimental animals, about 2/3 of MOC axons cross the midline and innervate the opposite cochlea, 1/3 innervate the cochlea on the same side, and a small fraction innervate both cochleae. The proportion of crossed vs. uncrossed axons in humans is unknown. Most MOC neurons receive sound-driven inputs from both cochlear nuclei with the strongest input from the contralateral side (The recent suggestion that the MOC reflex is driven primarily by Type-II auditory-nerve (AN) fibers is almost certainly wrong – Froud et al., 2015; Maison et al, 2016). MOC neurons with crossed axons are driven mostly by sound in the opposite ear and form the ipsilateral (double crossed) MOC reflex. MOC neurons with uncrossed axons form the contralateral reflex (the signal crosses in the inputs to the MOC neurons). There are no known differences in the OHC synapses of the ipsilateral vs. contralateral MOC reflexes, but their distributions along the cochlea are different. Compared to ipsilateral-reflex axons, contralateral-reflex axons innervate OHCs over a wider span along the cochlea that extends more apically (Brown, 2014).

One aspect of MOC innervation that is not well understood is the distribution of MOC innervation around the characteristic frequency (CF) of the MOC fiber. MOC innervation of the cochlea is tonotopic (i.e. each MOC fiber innervates a cochlear region tuned to the MOC fiber's CF). An individual MOC fiber innervates OHCs located both apically and basally around the cochlear CF region of the MOC fiber (Brown, 2014). Considerable evidence indicates that cochlear amplification takes place only basal of CF, so the MOC innervation that is apical of CF doesn't help in reducing the gain at the MOC fiber's CF. The implication is that MOC feedback is not anatomically arranged to be frequency specific and instead also affects nearby cochlear frequency regions.

LOC cell bodies are located in and near the lateral superior olivary (LSO) nucleus. LOC neurons have unmyelinated axons that synapse on the dendrites of AN fibers under inner hair cells (IHCs). LOC axons go predominantly to the cochlea on the same side as the axon's cell body. Since LOC axons are thin and unmyelinated, they are difficult to record from or electrically stimulate. Consequently, little is known about when they are activated or what they do to AN firing. Unmyelinated axons conduct action potentials slowly, and the effects attributed to LOC synapses are slow, i.e. they take place over minutes.

Efferent fibers have several roles in the development of normal auditory anatomy (e.g. Yin et al., 2014; Clause et al., 2017; reviewed by Nouvian et al., 2015).

2.2. Efferent action in the cochlea

MOC synapses release acetylcholine (ACh) onto specialized ($\alpha9/\alpha10$) ACh receptors (ACHRs) on the baso-lateral walls of OHCs (reviewed by Wersinger and Fuchs, 2011). Activated $\alpha9/\alpha10$ ACHRs allow Ca^{++} ions to enter the OHCs and these Ca^{++} ions activate nearby channels that allow K^{+} ions to flow into and hyperpolarize the OHCs. These Ca^{++} ions can also cause the release of Ca^{++} from local Ca^{++} stores, which increases the synaptic effect. The multistep increase in K^{+} flow into OHCs takes time and is the main determiner of the time course of MOC effects (~100 ms build up and decay times).

Activation of MOC synapses does two major things: it increases the OHC's basolateral conductance and it hyperpolarizes the OHCs. Increasing OHC basolateral conductance shunts OHC-stereocilia mechano-electric-transduction (MET) receptor current from flowing through the normal OHC basolateral conductance, thereby reducing the OHC voltage change and the resultant somatic motility and cochlear amplification. Hyperpolarizing OHCs is also thought to reduce somatic motility and cochlear amplification by moving the OHC voltage-to-length-change function to a less favorable operating point.

LOC synapses release ACh and several other neurotransmitters and neuromodulators, notably dopamine. There is evidence for two subgroups of LOC synapses: ACh synapses and dopamine synapses (Darrow et al., 2006b). Indirectly stimulating LOC axons increased or decreased AN-fiber firing, depending on where the neural stimulation was done (Groff and Liberman, 2003). It is tempting to think that ACh produces one of these effects and dopamine produces the other, but this has not been established. In addition to LOC effects on AN coding, an important function (perhaps the main function) of LOC efferents is to reduce damage to AN fibers from

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