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Motor-related signals in the auditory system for listening and learning

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In the auditory system, corollary discharge signals are theorized to facilitate normal hearing and the learning of acoustic behaviors, including speech and music. Despite clear evidence of corollary discharge signals in the auditory cortex and their presumed importance for hearing and auditory-guided motor learning, the circuitry and function of corollary discharge signals in the auditory cortex are not well described. In this review, we focus on recent developments in the mouse and songbird that provide insights into the circuitry that transmits corollary discharge signals to the auditory system and the function of these signals in the context of hearing and vocal learning.

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Introduction

Sensation often begets movement, pointing to a flow of information within the brain from sensory to motor regions. Perhaps less obviously, most behaviors also engage information flow in the opposite direction, in the form of motor-related corollary discharge signals that infiltrate sensory regions of the brain [1–4] (Figure 1). In the auditory system, corollary discharge signals are theorized to facilitate normal hearing by suppressing the responses of auditory neurons to movement-related auditory feedback [1]. Moreover, corollary discharge signals that accurately predict the expected auditory consequences of one's own movements (as posited for forward models of speech learning) can be compared with movement-related feedback to generate error signals, which are critical for learning to make movements with precise acoustic outcomes, including speech and music [5–7]. Despite clear evidence of corollary discharge signals in the auditory cortex and their presumed importance for hearing and auditory-guided motor learning, major questions regarding the form and function of corollary discharge signals in the auditory cortex remain unresolved.

What are the synaptic and circuit mechanisms by which movement-related corollary discharge signals modulate auditory cortical activity? Auditory cortical activity is often suppressed during movements including vocalization, but it is unknown whether suppression is due to increased inhibition, withdrawal of excitation, or some combination of both.

What are the circuits that convey corollary discharge signals to the auditory cortex? Although evidence for movement-related modulation of auditory cortex is pervasive, the source of movement-related signals that can be detected in the auditory cortex have remained a matter of speculation.

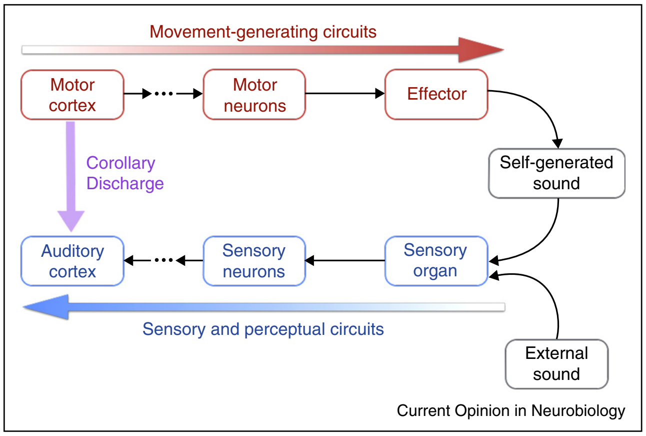
How do corollary discharge signals in the auditory system facilitate motor learning? Corollary discharge signals in the auditory cortex likely serve many roles, including helping us to learn complex acoustic behaviors, yet the causal role for corollary discharge signals in auditory-guided motor learning remains untested.

Recent studies in mice and songbirds have begun to provide answers to these questions, aided by advances in techniques for monitoring synaptic activity in freely behaving animals, improved behavioral quantification, and the experimental capacity to manipulate activity within defined neuronal populations. In particular, work in the mouse has begun to uncover the synaptic and circuit mechanisms by which motor and auditory signals are integrated in the brain, while studies using songbirds have shed light on how error-related information arising from forward interactions impinges on error correction circuitry to facilitate motor learning. In this review, we focus on recent developments in the mouse and songbird that provide a better understanding of how corollary discharge signals in the auditory system function during naturalistic behaviors.

Neural signatures of movement in the auditory cortex

Movement-related signals are likely to modulate auditory processing at many levels of the auditory neuraxis and even at the auditory periphery, as evidenced by the contraction of middle ear muscles during vocalization [8]. Despite the distributed nature of these signals, several reasons

Figure 1



The auditory system processes environmental sounds as well as sounds generated by our own movements. Motor-related corollary discharge signals that modulate the auditory cortex during movement are speculated to facilitate the detection of environmental cues and the learning of complex auditory-guided behaviors.

motivate a focus on corollary discharge signals at the cortical level, including the important role of cortical regions in speech and language [9–11], the pronounced capacity of cortical circuits for learning-related plasticity [12–14], and the strong suspicion that dysfunctional corollary discharge circuits in the cortex give rise to auditory hallucinations and certain forms of tinnitus [15]. In support of this focus, auditory cortical activity in humans and non-human primates is often suppressed during and before vocalization [1,5], manual musical gestures [16,17•,18], and non-musical movements [19,20], consistent with a motor origin. Notably, responses to vocalizations are most strongly suppressed when the sounds that the subject hears match the expected consequences, suggesting an acoustic specificity to corollary discharge signals at the level of the cortex [21]. Recent studies reveal that movement-related changes in auditory cortical activity in mice bear close parallels to those observed in humans and other primates. In both head-fixed and unrestrained freely behaving mice, spontaneous and tone-evoked firing rates of auditory cortical excitatory neurons are suppressed prior to and during movement, the latter indicating a divisive normalization of sound-evoked responses during movement that spans the mouse hearing range [22••,23•]. Moreover, many different types of movements, including grooming, locomotion, and vocalization, trigger changes in auditory cortical activity and sensory responsiveness [22••]. Therefore, in mice and humans, many behaviors, and not only vocalization, can modulate auditory cortical activity.

Synaptic and circuit mechanisms of corollary discharge in the auditory cortex

In addition to recapitulating key aspects of movement-related modulation of auditory cortical activity first observed in humans and other primates, studies in mice open the door to a range of experimental techniques that can shed light on the circuit and synaptic mechanisms through which corollary discharge signals suppress the auditory cortex during movement. In fact, recent studies using intracellular and extracellular recording combined with optogenetic methods in freely behaving mice provide evidence that movement-related signals actively suppress auditory cortical activity through a combination of mechanisms including increased activity in local inhibitory circuits [22••] and decreased excitatory drive from the thalamus (Williamson R *et al.*, Annual Meeting of the Society for Neuroscience (Washington, DC, 2014), submitted for publication) and from within the auditory cortex [23•].

Unlike extracellular recordings, intracellular recordings can resolve the activity of a neuron's synaptic inputs and enable measurement of a cell's input impedance and intrinsic excitability, all of which can be used to elucidate circuit mechanisms through which corollary discharge signals act in the auditory cortex. Intracellular recordings in head-fixed and unrestrained mice reveal that prior to and throughout movement, the membrane potential of auditory cortical excitatory neurons becomes much less variable, and these changes are accompanied by a decrease in input impedance and intrinsic excitability [22••]. These alterations in membrane properties are all signatures of postsynaptic inhibition, suggesting that corollary discharge signals drive activity in local inhibitory networks. In the auditory cortex of the mouse, parvalbumin-positive (PV+) inhibitory interneurons are known to provide strong inhibitory input onto excitatory neurons, providing a potential source of postsynaptic inhibition during movement [24]. However, whereas some studies indicate that PV+ interneurons show increased activity during movement ([22••]; McGinley MJ *et al.*, Annual Meeting of the Society for Neuroscience (Washington, DC, 2014), submitted for publication), another study concluded that PV+ interneurons decrease their activity during movements [23•]. These discrepancies may reflect the different time windows over which PV+ neural activity was measured: Schneider *et al.* detected transient increases in PV+ firing rates that began prior to movement and persisted into early stages of a locomotor bout, whereas Zhou *et al.* detected decreased PV+ firing rates when activity was averaged throughout an entire locomotor bout. One possibility is that transient increases in PV+ activity near the time of movement onset may induce more prolonged suppression of excitatory neurons, and that PV+ activity may rebalance with decreased levels of recurrent excitatory drive during later stages of sustained locomotion. In fact, rebalancing of excitatory and inhibitory currents has been observed in the auditory cortex during locomotion, consistent with this idea [23•].

Although local inhibition accounts for decreased responsiveness to acoustic stimuli within the auditory cortex,