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The dominance of inhibition in the inferior colliculus

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ABSTRACT

Almost all of the processing that occurs in the various lower auditory nuclei converges upon a common target in the central nucleus of the inferior colliculus (ICc) thus making the ICc the nexus of the auditory system. A variety of new response properties are formed in the ICc through the interactions among the excitatory and inhibitory inputs that converge upon it. Here we review studies that illustrate the dominant role inhibition plays in the ICc. We begin by reviewing studies of tuning curves and show how inhibition shapes the variety of tuning curves in the ICc through sideband inhibition. We then show how inhibition shapes selective response properties for complex signals, focusing on selectivity for the sweep direction of frequency modulations (FM). In the final section we consider results from in vivo whole-cell recordings that show how parameters of the incoming excitation and inhibition interact to shape directional selectivity. We show that post-synaptic potentials (PSPs) evoked by different signals can be similar but evoke markedly different spike-counts. In these cases, spike threshold acts as a non-linear amplifier that converts small differences in PSPs into large differences in spike output. Such differences between the inputs to a cell compared to the outputs from the same cell suggest that highly selective discharge properties can be created by only minor adjustments in the synaptic strengths evoked by one or both signals. These findings also suggest that plasticity of response features may be achieved with far less modifications in circuitry than previously supposed.

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1. Introduction

The inferior colliculus occupies a strategic position in the ascending auditory system. Almost all of the processing that occurs in the various lower auditory nuclei converges upon a common target in the central nucleus of the inferior colliculus (ICc) thus making the ICc the nexus of the auditory system (Casseday et al., 2002; Oliver and Huerta, 1992; Pollak and Casseday, 1986). The inputs to the ICc arise from a number of monaural lower nuclei that receive innervation from only one ear and from several binaural lower nuclei whose response properties are influenced by stimuli presented to both ears. The axonal projections from some of those nuclei, such as the dorsal cochlear nucleus (Davis, 2002; Malmierca et al., 2005b; Semple and Aitkin, 1980) and medial superior olive are purely excitatory (Davis, 2002; Glendenning et al., 1992; Semple and Aitkin, 1980). However the innervation from others, the dorsal nucleus of the lateral lemniscus (DNLL) and the columnar division of the ventral nucleus of the lateral lemniscus (VNLLc) are either purely inhibitory or, as in the case of the lateral superior olive (LSO) and intermediate nucleus of the lateral lemniscus (INLL), are a mixture of excitatory and inhibitory projections (Adams and Mugnaini, 1984; Bajo et al., 1999; Glendenning et al., 1992; Malmierca et al., 1998; Riquelme et al., 2001; Vater et al., 1997; Winer et al., 1995). It is also noteworthy that some of the inhibitory projections are glycinergic while others are GABAergic, where the number of inhibitory projections is at least as large, if not larger, than the excitatory projections (Winer et al., 1995).

The net result of these convergences is that a variety of new response properties are either formed *de novo* in the ICc or response properties that have been formed in lower nuclei are sharpened or further modified in the ICc. The constructions of new response properties or modifications of properties constructed below are due to the interactions among the excitatory and inhibitory inputs to the

Abbreviations: DCN, dorsal cochlear nucleus; DNLL, dorsal nucleus of the lateral lemniscus; EPSP, excitatory post-synaptic potential; FM, frequency modulation; ICc, central nucleus of the inferior colliculus; INLL, Intermediate nucleus of the lateral lemniscus; IPSP, inhibitory post-synaptic potential; LSO, lateral superior olive; MSO, medial superior olive; mV, millivolt; PSP, post-synaptic potential; STRF, spectrotemporal receptive field; VNLLc, columnar division of the ventral nucleus of the lateral lemniscus.

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ICc. The role of inhibition is difficult to overemphasize, as the selective features in the vast majority of ICc cells are either reduced or completely eliminated when inhibition is blocked by the iontophoretic application of receptor blockers (Casseday et al., 2000; Davis et al., 2003; Faingold et al., 1991; Nataraj and Wenstrup, 2005; Palombi and Caspary, 1996; Park and Pollak, 1993b; Sanchez et al., 2007, 2008) or when the inhibitory innervation from a lower source is reversibly inactivated (Burger and Pollak, 2001; Faingold et al., 1993; Malmierca et al., 2005a, 2003).

Here we review studies that illustrate the dominant role inhibition plays in the ICc. We begin by reviewing studies of tuning curves and show how inhibition shapes the variety of tuning curves in the ICc through sideband inhibition. We then show that inhibition shapes selective response properties for complex signals, and in the final section we consider how parameters of the incoming excitation and inhibition interact to shape discharge selectivity in the ICc.

The response feature that we focus on is selectivity for sweep direction of frequency modulations (FM), and how inhibition sculpts that selectivity. We focus on directional selectivity since FMs are a universal component of animal communication signals (Bohn et al., 2008, 2009; Doupe and Kuhl, 1999; Holy and Guo, 2005; Portfors et al., 2009; Ryan, 1983; Wang et al., 1995), including human speech, and preferences for FM sweep direction are a selective feature commonly seen in the mammalian auditory system (Fuzessery, 1994; Nelken and Versnel, 2000; Poon et al., 1991; Razak and Fuzessery, 2006; Zhang et al., 2003). Additionally, directional preferences for FM are an emergent property of the ICc and have been the subject of numerous studies that have provided insights into the mechanisms underlying its generation (Andoni et al., 2007; Felsheim and Ostwald, 1996; Fuzessery and Hall, 1996; Gaese et al., 2006; Gittelman et al., 2009; Poon and Chiu, 2000; Poon et al., 1991; Suga, 1968).

There are two principal mechanisms that have been proposed in previous studies to explain response preferences in the ICc for FM direction, as illustrated in Fig. 1. Both incorporate differences between the timing of inputs evoked by the preferred and null FMs (Brimijoin and O'Neill, 2005; Casseday et al., 2002; Covey and Casseday, 1999; Fuzessery, 1994; Poon et al., 1991; Suga, 1968; Suga, 1973; Suga and Schlegel, 1973; Yue et al., 2007). Further, both assume that the excitatory and inhibitory inputs to the IC are non-directional, and thus the preferred and null FMs evoke equally strong excitations and that both FMs evoke equally strong inhibitions. One hypothesis posits a timing asymmetry between excitation and inhibition, where the preferred FM activates excitation first, whereas the null FM activates inhibition first. When excitation arrives first, it is initially unopposed by inhibition and thus evokes discharges. When inhibition arrives first or is coincident with the excitation, the inhibition acts to reduce or even completely cancel the excitation thereby suppressing discharges. The second hypothesis posits that directionality is generated by the relative coincidence in the arrival of excitatory (or inhibitory) inputs. More coincident excitatory arrivals generate a higher amplitude EPSP, whereas less coincident arrivals generate a longer response of lower amplitude. Thus, compared to the null, the preferred FM would evoke more coincident excitatory inputs, and/or less coincident inhibitory inputs. The two hypotheses outlined above are not mutually exclusive. There is however, considerable evidence to support the hypothesis of timing asymmetries of excitation and inhibition (Andoni et al., 2007; Fuzessery and Hall, 1996; Fuzessery et al., 2006; Koch and Grothe, 1998), whereas the second, coincidence model, is based either on a theoretical possibility or on Rall's model of synaptic integration along dendrites (Rall, 1969), in a manner similar to the proposal for FM directionality in octopus cells in the cochlear nucleus (Golding et al., 1995).

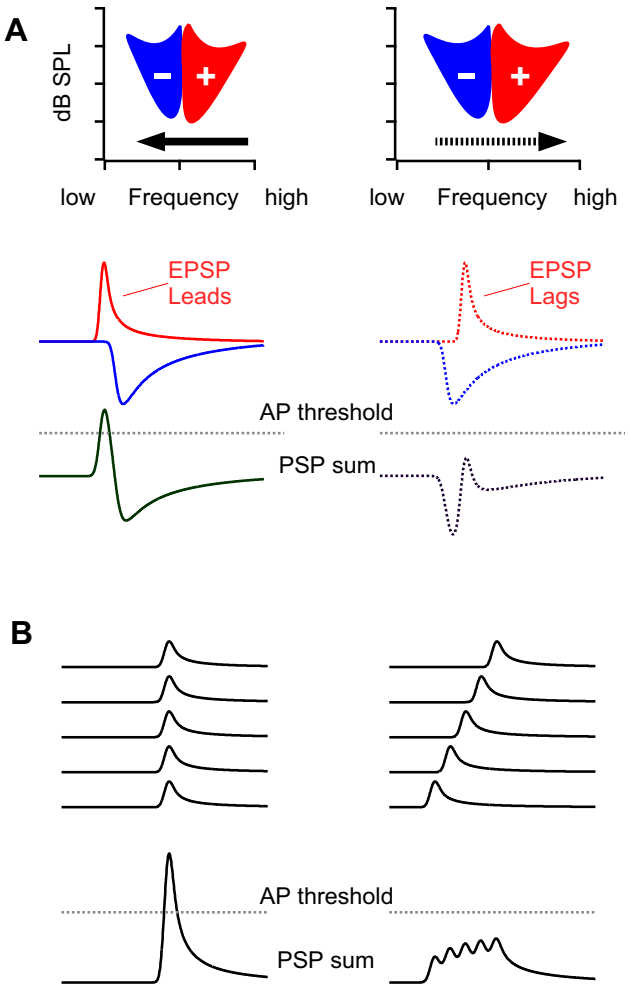

Fig. 1. Schematic illustration of the two major hypotheses for FM directional selectivity. A: asymmetric timing of excitation and inhibition. A downward sweeping FM in this case stimulates the cell's excitatory frequencies first and then stimulates inhibitory region on the low frequency flank of the excitatory region. Excitation (red EPSPs) is evoked first, and since excitation occurs before inhibition (blue IPSP), the excitation evokes a suprathreshold EPSP that generates spikes. An upward sweeping FM first enters the inhibitory region (blue) and evokes inhibition that suppresses the following excitation, resulting in a subthreshold PSP. B: Coincidence hypothesis that proposes that the frequencies in an FM sweeping in one direction, downward in this case, evokes a series of excitatory inputs that arrive at the target cell coincidentally. The summation of the inputs that arrive simultaneously evoke a suprathreshold EPSP. In contrast, an FM sweeping in the opposite direction, upward in this case, evokes a series of excitatory inputs with different latencies. The inputs arrive at the target cell at successive times. The summation of the staggered inputs generates a PSP of longer duration but lower amplitude than the downward FM.

Although FM directionality has been studied in a variety of mammals, the majority of studies have been conducted on bats. Bats are hearing specialists and have well developed neural circuits that underlie their acoustic behaviors (Pollak and Casseday, 1986). Their auditory systems, however, are not unique. Indeed, their brainstem auditory systems have the same nuclei, cell types, connections and the same mechanisms for processing information that are possessed by all other mammals (Feng and Vater, 1985; Pecka et al., 2007; Pollak and Casseday, 1986; Pollak et al., 1995; Winer et al., 1995). What distinguishes the auditory systems of bats are not novel mechanisms, but rather that some common structural and mechanistic features are more pronounced in their auditory systems than in other mammals. One pronounced response feature is the high proportion of FM directional cells in their ICc (Andoni et al., 2007; Brimijoin and O'Neill, 2005;

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