



## Review

## Development of auditory cortical synaptic receptive fields

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## ABSTRACT

The central nervous system is plastic throughout life, but is most sensitive to the statistics of the sensory environment during critical periods of early postnatal development. In the auditory cortex, various forms of acoustic experience have been found to shape the formation of receptive fields and influence the overall rate of cortical organization. The synaptic mechanisms that control cortical receptive field plasticity are beginning to be described, particularly for frequency tuning in rodent primary auditory cortex. Inhibitory circuitry plays a major role in critical period regulation, and new evidence suggests that the formation of excitatory–inhibitory balance determines the duration of critical period plasticity for auditory cortical frequency tuning. Cortical inhibition is poorly tuned in the infant brain, but becomes co-tuned with excitation in an experience-dependent manner over the first postnatal month. We discuss evidence suggesting that this may be a general feature of the developing cortex, and describe the functional implications of such transient excitatory–inhibitory imbalance.

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## Contents

1. Introduction.....	2105
2. Subcortical development.....	2106
3. Development of AI maps and receptive fields.....	2106
4. Tonotopic map and receptive field plasticity.....	2107
5. Synaptic receptive field plasticity in AI.....	2108
6. Potential pre-balancing of excitation and inhibition in rat AI.....	2110
7. Discussion.....	2111
References.....	2111

## 1. Introduction

The natural world is complex and dynamic. In order for an animal to survive and successfully navigate in such environments, the brain must be able to rapidly process and operate on a diverse range of sensory stimuli. Some components of the nervous system seem to be genetically specified and perinatally hard-wired, particularly in the peripheral sensory epithelium (Sobeih and Corfas, 2002; Harris and Rubel, 2006). More central regions, however, have been found to rely on electrical activity and sensory experience to instruct or control the development of synaptic transmission and the organization of receptive fields (Katz and Shatz, 1996; Sanes and Bao, 2009). This seems especially true in the primary auditory cortex (AI), where manipulations of early acoustic experience produce a

range of profound and lasting effects on the structure and function of AI neurons and synapses.

Here we review the critical factors for developmental plasticity of AI synaptic receptive fields. We begin by summarizing important studies on the formation of the subcortical auditory system, as normative AI development presumably requires prior organization of the thalamus and other upstream regions. We then briefly review previous work on the establishment of AI tonotopy and spiking receptive fields, before describing the processes that shape the underlying synaptic receptive fields of AI neurons. We focus here on the postnatal development of excitatory–inhibitory balance for frequency tuning in rat AI. Although there are recent confusing data on the degree to which AI inhibitory inputs are tuned in neonatal AI (Dornn et al., 2010; Sun et al., 2010), we aim to clarify this issue by discussing the findings and methods of these and other related studies in some detail. Collectively, these data suggest that various receptive field components or functional sectors of AI develop in distinct stages or at different rates, depending on position within

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the network and the computational complexity of the postnatal acoustic world.

## 2. Subcortical development

The rodent auditory system is altricial, developing throughout the first postnatal month (Sanes and Bao, 2009). Hearing onset in rodents such as rats and mice occurs around postnatal day (P) 11, although bone conduction-related events can be measured as early as P7 (Geal-Dor et al., 1993). For comparison, the human auditory system is functional in prenatal infants, and auditory responses can be evoked *in utero* as early as the 27th prenatal week (Moore and Linthicum, 2007). Regardless of the functional onset time, auditory development in most species studied is a protracted process. This extended and delayed maturation presumably allows central regions of the nascent auditory system to form connections and refine synaptic strengths in a manner that reflects the acoustical properties and behavioral significance of the sensory environment (Keuroghlian and Knudsen, 2007), while more peripheral areas develop precise connections independently of auditory experience (Rubel and Fritzsche, 2002).

Much of the rodent subcortical auditory system is mature by P11–P12. The cochlear microphonic can be recorded in rats as early as P8 (Uziel et al., 1981), and cochlear cells are spontaneously active from P0 to P10 (Tritsch and Bergles, 2010). Perhaps analogous to the hypothesized function of retinal waves (McLaughlin et al., 2003), this spontaneous activity is potentially important for pre-patterning the auditory periphery before hearing onset, and is suddenly curtailed in inner supporting cells upon hearing onset. Projections from the auditory brainstem to midbrain in rat are present at P4 and mature throughout P4–P12 (Fathke and Gabriele, 2009). A comparable process seems to occur at the same ages for thalamocortical connections from the ventral division of the medial geniculate nucleus into rodent AI (Lund and Mustari, 1977; Robertson et al., 1991). Neurogenesis and synapse formation in the inferior colliculus seems to occur early in perinatal life, and response properties of these midbrain neurons are largely mature soon after hearing onset (Brunso-Bechtold and Henkel, 2005), with lower thresholds and higher characteristic frequencies emerging at later ages (Aitkin and Moore, 1975), e.g., P13–P20 in the house mouse (Romand and Ehret, 1990). Therefore the subcortical circuitry is in place for robust tone-evoked responses to be detected in postnatal AI at ~P12, with refinement of receptive fields continuing through the first month of life in the rodent auditory system.

## 3. Development of AI maps and receptive fields

Despite this early wiring of the upstream auditory pathway, some physiological properties of AI remain immature throughout the first three postnatal weeks or longer. This is likely a consequence of the high level of plasticity inherent in AI: the auditory cortex is among the most plastic regions of the auditory system, rapidly re-tuning in response to changes of acoustic input (Buonomano and Merzenich, 1998). Plasticity seems greatest during neonatal critical periods, which are developmental epochs during which neural circuits are intrinsically sensitive to the acoustic parameters of the external environment (Hensch, 2005; Sanes and Bao, 2009). Critical periods in the auditory cortex usually last for a few days or weeks, beginning just after the onset of hearing. Recent compelling evidence suggests that various receptive field properties and distinct brain regions have different critical periods that are overlapping or staggered (Insanally et al., 2009; Popescu and Polley, 2010). In this way, lower level representations of the auditory world can be constructed, refined, and stabilized, enabling more complex stimuli to then be processed by cortical cir-

cuitry. As the excitatory inputs are mostly well-formed by hearing onset, we hypothesize that this protracted developmental process depends fundamentally on the delayed maturation of intracortical inhibitory circuitry (Dorn et al., 2010), analogous to the development of visual cortical receptive field properties such as ocular dominance (Hensch, 2005).

Critical period development and plasticity of AI have been most thoroughly characterized *in vivo* at the level of spiking receptive fields and tonotopic map organization. In adult rats, AI is functionally defined as having short latency responses (5–20 ms from stimulus onset), with high reliability and well tuned to pure tones (Sally and Kelly, 1988; Polley et al., 2007). Prior to hearing onset (P11), tone-evoked responses cannot be detected in neonatal rat AI, except possibly via bone conduction (Geal-Dor et al., 1993). Immediately afterward, AI consists of a relatively small core region at P11, tuned to mid-range frequencies (de Villers-Sidani et al., 2007), and surrounded by a large responsive but untuned area (Zhang et al., 2001). At this young age, spike latencies can be longer (20–40 ms) and thresholds tend to be higher (50–60 dB SPL). After P11, the well-tuned sector of AI becomes progressively larger (Fig. 1A). By P13–P14, the size, tonotopic gradient, and responsiveness (including spike thresholds of ~20 dB SPL) of rat AI is equivalent to that in adult animals (de Villers-Sidani et al., 2007). However, response latencies can still be relatively long, taking until P20–P25 to reach mature levels. Similar patterns of postnatal cortical development can be observed in other mammalian species – e.g., cat (Brugge et al., 1988; Bonham et al., 2004), chinchilla (Pienkowski and Harrison, 2005), ferret (Mrsic-Flogel et al., 2006), and bat (Vater et al., 2010) – although there are important differences in the details of the development and mature organization of AI in each of these animal models, including the exact pre- and postnatal ages at which auditory system development occurs (Romand, 1997).

This increase in effective size of rat AI is at least partially a consequence of how AI itself is physiologically defined: as previously unresponsive neurons, poorly tuned cells, or cells with abnormally long latency take on aspects of mature AI cells, they become included within the experimentally determined map of AI (Zhang et al., 2001). Therefore, tonotopic map formation necessarily develops in parallel with the organization of individual frequency–intensity receptive fields in rat AI (Fig. 1A). By ~P21, frequency–intensity receptive fields appear equivalent to those recorded in the adult brain. Prior to this date, some reports found that neurons were usually narrowly tuned (de Villers-Sidani et al., 2007; Insanally et al., 2009), while others observed that neonatal tuning was broad on average (Zhang et al., 2001). An examination of other statistics besides bandwidth (including latency, threshold, and overall area) reveals that the development of these properties of rat auditory cortical spiking receptive fields has been inconsistently reported in the field (compare Zhang et al., 2001; Chang et al., 2005; de Villers-Sidani et al., 2007; Insanally et al., 2009; Sun et al., 2010). The reasons for such heterogeneity are unclear, but could be related to differences in rodent neonatal auditory experience, or subtle variation in mapping, extracellular recording, and criteria for defining AI (see Section 6 below).

Other aspects of AI receptive fields may develop at different, slower rates. For example, the extent of sideband suppression in AI neurons seems to be larger in young animals than older animals, and the developmental progression of sideband suppression continues past the first postnatal month. Suppression can be measured by presenting a pair of pure tonal stimuli simultaneously; in this case, the responsive area of the frequency–intensity receptive field is reduced at the edges. The extent of simultaneous two-tone suppression remains broad until P45 (Chang et al., 2005). This developmentally delayed suppression of AI responses is regulated to some degree by GABAergic inhibition, as iontophoretic application of bicuculline (a GABA<sub>A</sub> receptor antagonist) preferentially

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