

Experience-dependent development of vocalization selectivity in the auditory cortex^{a)}

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Vocalization-selective neurons are present in the auditory systems of several vertebrate groups. Vocalization selectivity is influenced by developmental experience, but the underlying mechanisms are only beginning to be understood. Evidence is presented in this review for the hypothesis that plasticity of timing and strength of inhibition is a mechanism for plasticity of vocalization selectivity. The pallid bat echolocates using downward frequency modulated (FM) sweeps. Nearly 70% of neurons with tuning in the echolocation frequency range in its auditory cortex respond selectively to the direction and rate of change of frequencies present in the echolocation call. During development, FM rate selectivity matures early, while direction selectivity emerges later. Based on the time course of development it was hypothesized that FM direction, but not rate, selectivity is experience-dependent. This hypothesis was tested by altering echolocation experience during development. The results show that normal echolocation experience is required for both refinement and maintenance of direction selectivity. Interestingly, experience is required for the maintenance of rate selectivity, but not for initial development. Across all ages and experimental groups, the timing relationship between inhibitory and excitatory inputs explains sweep selectivity. These experiments suggest that inhibitory plasticity is a substrate for experience-dependent changes in vocalization selectivity. © 2010 Acoustical Society of America. [DOI: 10.1121/1.3377057]

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I. MODEL SYSTEMS TO STUDY DEVELOPMENT OF VOCALIZATION SELECTIVITY

Vocalization-selective neurons are present in several vertebrate groups (Capranica, 1972; Fuzessery and Feng, 1983; Margoliash and Konishi, 1985; Margoliash, 1986; Ohlemiller *et al.*, 1996; Wang, 2000; Klug *et al.*, 2002; Suta *et al.*, 2003). There is considerable interest in determining how vocalization-selective neurons develop. In songbirds, it is known that vocalization selectivity undergoes developmental changes in parallel with maturation of vocalizations (Doupe and Konishi, 1991; Doupe, 1997; Solis and Doupe, 1997). Perhaps because of their complex, multi-syllable structure, the mechanisms that shape selectivity for songs are only beginning to be understood (Lewicki, 1996; Rosen and Mooney, 2005). How these mechanisms change during development is, however, unclear. The development of neural selectivity for vocalizations in mammals has not received as much attention. In addition to the complexity of communication calls, selectivity for single calls is less pronounced in the mammalian auditory system (Glass and Wollberg, 1983; Wang, 2000; Klug *et al.*, 2002; Suta *et al.*, 2003) making it difficult to determine mechanisms that shape vocalization selectivity and to study their developmental changes. The bat

echolocation system may be a useful model to address this issue because of the relative simplicity of the echolocation call and strong neural selectivity for its parameters. Here we review a series of studies of the auditory cortex of the pallid bat to address the role of experience in the development of neural selectivity for echolocation calls.

II. PARALLEL AUDITORY PATHWAYS FOR TWO DIFFERENT BEHAVIORS

The pallid bat (*Antrozous pallidus*) is a gleaner bat that listens to prey-generated noise transients (5–40 kHz) to localize and hunt prey, while reserving echolocation for general orientation and obstacle avoidance (Bell, 1982; Fuzessery *et al.*, 1993; Barber *et al.*, 2003). To echolocate, these bats produce a 60 → 30 kHz downward frequency modulated (FM) sweep [1.5–5 ms duration, Fig. 1(a)]. The inferior colliculus (IC)-medial geniculate body (MGB)-cortex connections in the pallid bat auditory system are organized as parallel pathways that represent noise and echolocation calls in segregated regions (Fuzessery, 1994; Razak and Fuzessery, 2002; Razak *et al.*, 2007). In the IC, neurons in the central nucleus are selective for the rate and direction of FM sweeps used by the pallid bat. Neurons in the lateral IC are sensitive to noise transients (Fuzessery, 1994). In the auditory cortex, noise- and FM sweep-sensitive neurons are located in mostly segregated regions (Razak and Fuzessery, 2002). Nearly 70% of the neurons that are tuned to 30–60 kHz are selective for

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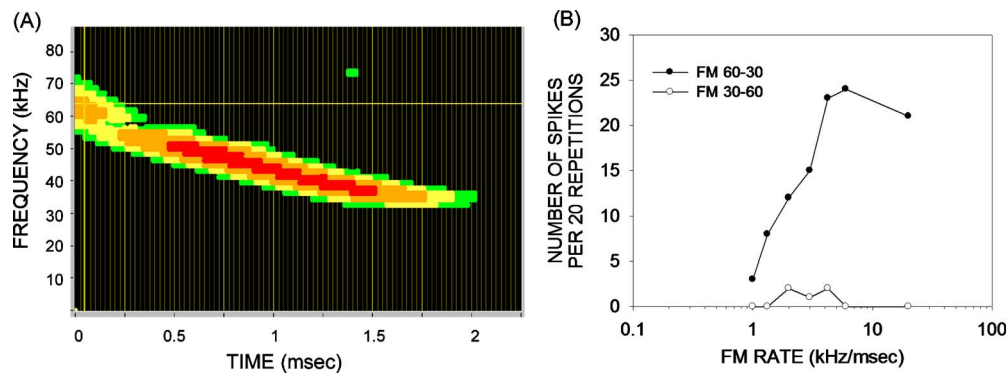


FIG. 1. (Color online) (a) Spectrograph of a typical pallid bat echolocation call—a downward FM sweep between 60–30 kHz, with duration ~ 2 ms. (b) A neuron selective for downward FM (60 \rightarrow 30 kHz) sweep with rate of change of frequencies >6 kHz/ms.

downward FM sweeps like the bat's own echolocation call [e.g., Fig. 1(b); Razak and Fuzessery (2006)]. FM sweep-selective neurons receive their ascending afferents from the supragenicular nucleus of the MGB, but not the ventral division (MGBv) whereas the noise-selective neurons receive theirs from the MGBv, but not the supragenicular (Razak *et al.*, 2007). Thus there is an emphasis on segregated processing of echolocation calls and prey-generated noise in the pallid bat auditory system.

The presence of a separate region in the auditory cortex wherein the vast majority of neurons are selective for the bat's echolocation call presents an ideal opportunity to examine how vocalization selectivity develops. In addition to the high incidence of selective neurons, another advantage of the pallid bat is that the development of echolocation behavior and auditory sensitivity has been studied (Brown *et al.*, 1978). This allows examination of development of neural selectivity within the context of behavioral development.

III. MECHANISMS UNDERLYING ECHOLOCATION CALL SELECTIVITY

Given that most neurons are selective for the direction and rate of FM sweeps used in echolocation, we first sought to examine the mechanisms underlying FM selectivity in adults. Auditory cortical neurons are similar to other sensory cortical neurons in that they have a center-surround excitatory-inhibitory receptive field (RF) organization. Asymmetries in surround (sideband) inhibition underlie FM sweep selectivity (Suga, 1965). In addition to the presence or absence of sideband inhibition, a key determinant of sweep selectivity is the relative arrival time of inhibition (Gordon and O'Neill, 1998; Razak and Fuzessery, 2006).

The spectrotemporal properties of inhibition can be determined using the two-tone inhibition (TTI) over time method (Fig. 2). By presenting two tones with different frequencies and delays between them [Fig. 2(a)], the frequency-delay combinations that result in inhibition of responses to an excitatory tone can be determined (Calford and Semple, 1995; Brosch and Schreiner, 1997; Gordon and O'Neill, 1998). The arrival time of inhibition can be inferred by presenting tone frequencies that evoke inhibition or excitation at different delays with respect to each other. If response suppression occurs even when the inhibitory tone is delayed

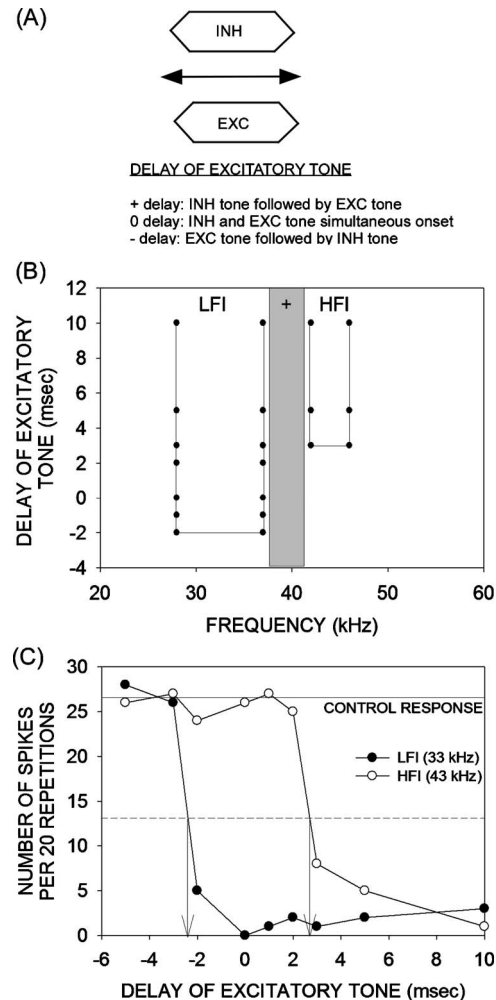


FIG. 2. The “two-tone inhibition over time” method used to determine arrival time and bandwidth of inhibitory sidebands. (a) In this method, an excitatory tone (EXC) is delayed or advanced with respect to an inhibitory tone (INH). The intensity of the two tones is the same. Simultaneous onset of the two tones is denoted as 0 ms delay. Delayed (earlier) onset of the excitatory tone with respect to the inhibitory tone is denoted as positive (negative) delay. (b) The TTI tuning curve shows frequency on the x-axis, and the delay of the excitatory tone on the y-axis. The gray bar shows the excitatory frequency tuning curve at the intensity at which the TTI test was performed. Inhibition occurring at negative delays arrived early, while inhibition occurring at positive delays arrived late. (c) The 50% arrival time of inhibition was the delay of excitatory tone at which an inhibitory tone caused a 50% decrease in control response (solid horizontal line, response to best frequency tone alone). The horizontal dashed line shows 50% of control response, while the vertical arrows indicate the 50% arrival time for two different inhibitory tones.

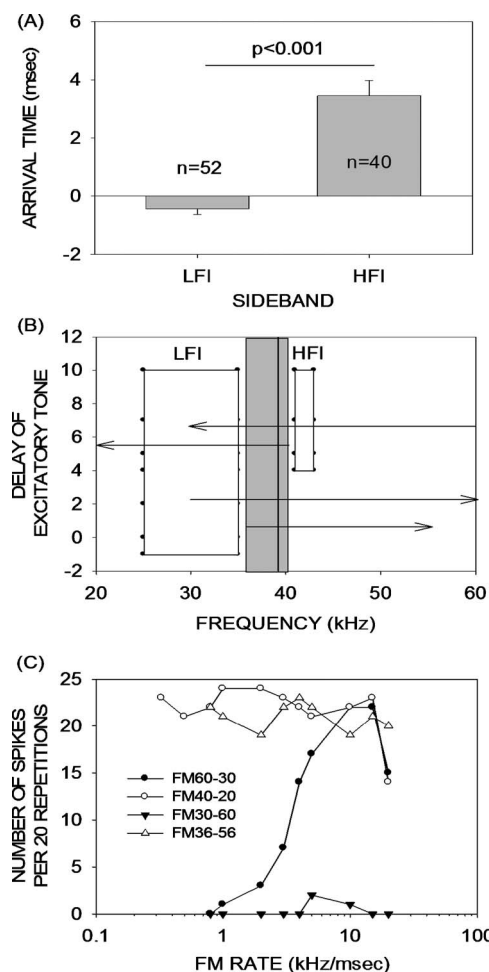


FIG. 3. Asymmetries in arrival time of inhibition shape FM sweep selectivity. (a) On average, LFI had an earlier arrival time (indicated by the negative mean—see Fig. 2) than HFI. N values show number of neurons. (b, c) sideband inhibition and FM selectivity of a cortical neuron. (b) This neuron had an early arriving LFI centered ~30 kHz and a late HFI centered ~42 kHz. Arrows denote various sweep bandwidths used to test FM selectivity. (c) The 60–30 kHz sweep was a downward sweep that included the HFI. The neuron was rate selective for this sweep with best responses ~10 kHz/ms. The 40–20 kHz sweep was a downward sweep that excluded HFI. The neuron was not rate selective for this sweep showing that the HFI was necessary to cause rate selectivity for downward sweeps. The 30–60 kHz upward sweep included the LFI and was unable to elicit much response from the neuron. The 36–56 kHz upward sweep excluded the LFI and elicited robust responses from the neuron showing that LFI was necessary for direction selectivity. Data reproduced from Razak and Fuzessery (2006)

relative to the excitatory tone (backward masking, negative delays in Fig. 2), then it can be inferred that inhibition arrived early. If inhibition occurs only when the inhibitory tone is presented before the excitatory tone (forward masking, positive delays in Fig. 2), then inhibition is delayed. The arrival time of inhibitory frequencies above (high-frequency inhibition, HFI) or below (low-frequency inhibition, LFI) the excitatory tone can be determined using this method [Figs. 2(b) and 2(c)].

In adult pallid bat auditory cortex neurons tuned to the echolocation range of frequencies, LFI arrives early, whereas HFI is delayed [e.g., Figs. 2(b) and 2(c); averages in Fig. 3(a); Razak and Fuzessery (2006)]. For an upward sweep, inhibition will be triggered and will arrive before excitation and thus will suppress responses. A downward sweep

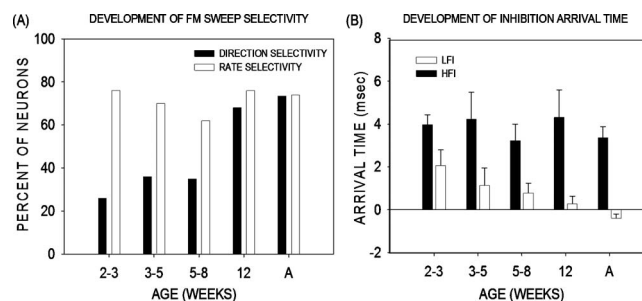


FIG. 4. Normal development of sweep selectivity and timing of inhibition. (a) FM rate selectivity was adult-like (a) from 2 weeks. Direction selectivity, however, was seen in only 25% of the neurons at 2 weeks. Direction selectivity reached adult-like values ~3 months postnatal. (b) Average arrival time of HFI was adult-like from 2 weeks. Average arrival time of LFI became progressively faster with age, reaching adult-like values ~3 months postnatal. Data reproduced from Razak and Fuzessery (2007).

traverses HFI before reaching excitation. However, because HFI is slow, an FM sweep with a fast rate of change of frequency will reach excitation before inhibition arrives. For slow sweeps, HFI will arrive before excitation. This will shape rate selectivity for downward FM sweeps. According to this model, removal of LFI from the sweep should eliminate direction selectivity [e.g., Figs. 3(b) and 3(c)]. Removal of HFI from the downward sweep should eliminate rate selectivity [e.g., Figs. 3(b) and 3(c)]. This prediction was met in ~80% of rate- and direction-selective neurons (Razak and Fuzessery, 2006). Thus the asymmetry in arrival time of LFI and HFI serves as the primary mechanism for rate and direction selectivity in the auditory cortex of the pallid bat.

Pharmacological studies also support the importance of arrival time of LFI/HFI for direction and rate tuning (Razak and Fuzessery, 2009). Ionophoresis of a GABA-A receptor antagonist (gabazine or bicuculline) reduces rate and direction selectivity in the majority of cortical neurons. The effect of the antagonists on sweep selectivity was predicted by their effects on two-tone inhibition. The implication of these data is that the presence and timing of inhibition is critical for FM sweep selectivity and that cortical neurons' FM selectivity depends to a large extent on local inhibition.

IV. DEVELOPMENT OF RESPONSE SELECTIVITY IN THE AUDITORY CORTEX

Given that the asymmetries in arrival time of LFI and HFI underlie FM direction and rate selectivity, we examined the time course of development of such asymmetries and sweep selectivity. The pallid bat begins to hear around P (postnatal day) 8. By P14, the hearing sensitivity becomes adult-like (Brown, 1976; Brown et al., 1978). The bat begins to fly ~P35 and is weaned ~P60. Echolocation calls become adult-like ~P20. We examined FM sweep selectivity and arrival times of inhibition of cortical neurons from P14 to P90 (Razak and Fuzessery, 2007).

FM rate selectivity was adult-like from P14. The percentage of downward FM rate selective neurons [Fig. 4(a)] and the preferred FM rates were similar across all age groups tested. The underlying mechanisms namely, the bandwidth and arrival time [Fig. 4(b)] of HFI, were also adult-like from P14. FM direction selectivity, however, was slow to develop

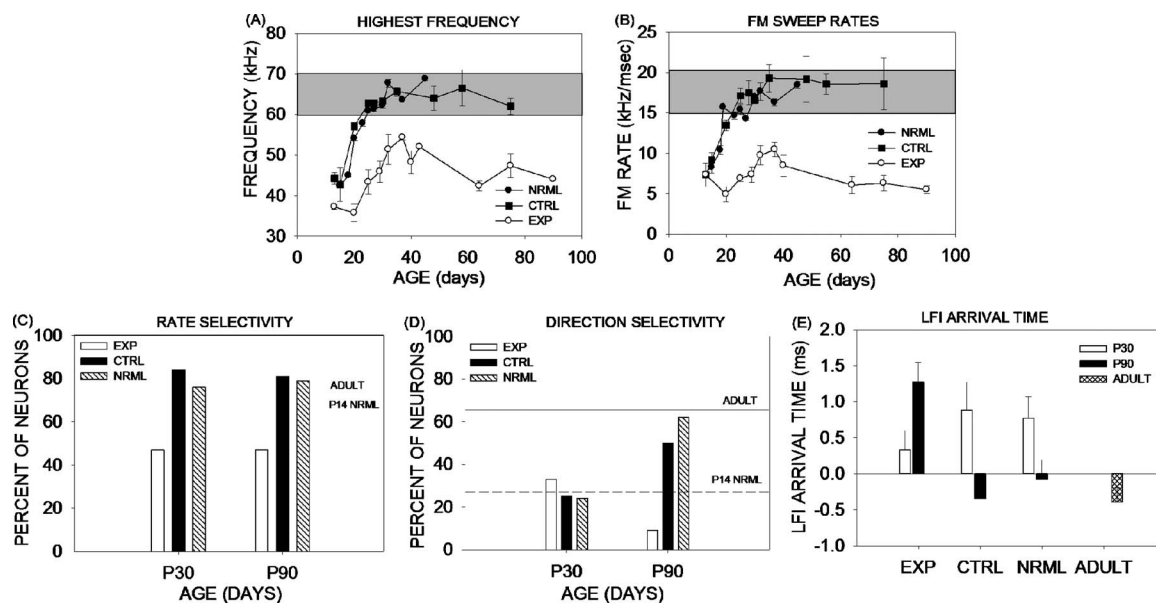


FIG. 5. Effect of larynx lesion on call properties and the effects of altered echolocation experience on FM rate selectivity. (a) Highest frequencies present in the echolocation calls of the three different groups studied. EXP—muted group; CTRL—control group; NRML—normal group. The gray bar denotes the adult range. (b) FM sweep rates present in the echolocation calls of the different groups studied. Gray bar denotes adult range. Data in (c) and (d) are mean \pm s.e. (c) FM rate selectivity was present in a significantly lower percentage of neurons in the muted group compared to control and normal groups. Rate selectivity was reduced compared to week old normal bats (dashed line) indicating that normal experience was required for maintenance of FM rate selectivity. (d) Direction selectivity was virtually absent in the P90 EXP group. It was even lower than the 2 week old normal group, indicating that normal experience was required for both development and maintenance of direction selectivity. (e) The arrival time of LFI in the normal and control groups approached adult-like values \sim P90. In the EXP group, however, LFI arrival time was more delayed than in the other groups. This shows normal echolocation experience is required to shape millisecond-level changes in arrival time of inhibition.

[Fig. 4(a)]. Compared to \sim 70% direction-selective neurons in the adult, only \sim 25% of neurons were direction selective in P14 bats. The percent of neurons with direction selectivity became adult-like only after 12 months of age, well after the bat is weaned. The developmental changes in direction selectivity accompanied changes in the arrival time of LFI [Fig. 4(b)]. Average arrival time of LFI became progressively faster with development. At all developmental ages, most neurons with early arriving LFI were direction selective while those with either delayed LFI or no LFI were not direction selective. Taken together, this suggested that FM rate selectivity developed in an echolocation experience-independent manner, while development of FM direction selectivity in the vast majority of neurons is experience-dependent.

V. ROLE OF EXPERIENCE IN THE DEVELOPMENT OF ECHOLOCATION CALL SELECTIVITY

To test the above hypotheses, we compared the echolocation call selectivity of neurons in three groups of bats with different rearing experiences. The first group of pups, called “normal,” developed in the presence of other bats. These pups could hear echolocation calls produced by self, litter mates and adults. The second groups of pups, called “control” were isolated from \sim P10 (before development of sensitivity in the echolocation frequency range) and hand-raised. These bats could hear their own vocalizations, but not other bats. The third group of bats, called “experimental,” received either an injection of botulinum toxin (botox) into, or a heat lesion of, their laryngeal muscle \sim P10, and were raised in isolation from that time forward. These bats did not produce

normal echolocation calls during development [Figs. 5(a) and 5(b)]. In particular, the highest frequencies in calls were at lower frequencies in the experimental than in age-matched control and normal bats [Fig. 5(a)]. The FM rate was also significantly lower in the experimental pups [Fig. 5(b)]. FM rate and direction selectivity and arrival time of inhibition were compared across these groups at P30 and at P90.

Interestingly, the percent of FM rate selective neurons decreased significantly in the experimental groups at P30 and P90 [Fig. 5(c)]. Thus, although experience is not required for the initial development of FM rate selectivity, it is required for the continued maintenance of rate selectivity. As hypothesized, direction selectivity was almost completely eliminated in the experimental group at P90 compared to age-matched normal and control groups [Fig. 5(d)]. At P30, direction selectivity was present in $<30\%$ of neurons in all pup groups. At P90, the percent of direction-selective neurons was even lower than that at P30. These data suggest that normal experience is required for both *refinement* and *maintenance* of FM direction selectivity. Neural selectivity in the control group was similar to the normal group, suggesting “self-produced” echolocation calls are sufficient to shape normal response selectivity.

Given that sideband inhibition underlies FM sweep selectivity in the vast majority of neurons, the effects of experience on FM sweep selectivity may be mediated by altered properties of inhibition. A higher percentage of neurons in the experimental group (both P30 and P90) showed no sideband inhibition compared to control and normal (Razak et al., 2008). The average LFI arrival time in the experimental group was also delayed compared to the other two groups

[Fig. 5(e)]. While LFI arrival times became progressively shorter in the control and normal groups, it became longer in the experimental group between P30 and P90. Neurons with fast LFI exhibited direction selectivity in all groups, but there were fewer such neurons in the experimental group. Taken together, these data show that normal experience is required to make “millisecond-range” adjustments in temporal properties of inhibition to shape normal selectivity.

The sequence of studies reviewed here shows that asymmetries in arrival time of inhibition shapes FM rate and direction selectivity in the pallid bat cortex. FM rate and direction selectivity develop over different time courses, with rate selectivity emerging earlier and in an experience-independent manner. Normal experience with echolocation calls is required for both refinement and maintenance of direction selectivity, and for the maintenance of rate selectivity. The experience-dependent changes in FM sweep selectivity can be explained by changes in arrival time and strength of inhibition.

VI. SYNTHESIS AND FUTURE STUDIES

Experience is typically thought to play an important role in the refinement of neural response selectivity in sensory systems. Our data suggest that experience can also be important for *maintaining* response selectivity that was originally created in an experience-independent manner. Few other studies have looked at the role of experience in the maintenance of response properties. In ferrets, blocking retinal activity after eye-specific segregation has occurred in the lateral geniculate nucleus causes desegregation (Chapman, 2000), suggesting that activity is required for the maintenance of connectivity. In the superior colliculus of hamsters, receptive fields refine in the absence of light during development (Carrasco *et al.*, 2005). However, continued maintenance of the animals in the dark causes RF diameters to broaden, suggesting that light input is required for maintenance of RF size. The reduction in surround inhibition in hamsters maintained in the dark is suggestive of a role for inhibitory mechanisms as observed in the pallid bat cortex.

Another observation from these studies is that millisecond-level changes in arrival time of inhibition can have profound influence on response selectivity. This raises the question of how timing of inhibition is altered by experience. One possibility is that strength and timing of inhibitory inputs are related. That is, a delay in arrival time may be caused by a reduction in strength of the inhibitory input. In the rat auditory cortex, the timing of inhibitory currents varied monotonically with intensity of tones (Wu *et al.*, 2006). Preliminary data in the pallid bat auditory cortex show that increasing the intensity of the inhibitory tones with respect to the excitatory tones in the two-tone inhibition protocol can cause significant changes in arrival times (Razak *et al.*, 2008). Thus, a critical developmental event across sensory systems may be the matching of amplitudes of inhibitory and excitatory inputs.

Another possible mechanism for change in timing of inhibition and its effect on FM direction selectivity is spike-timing dependent plasticity. During development of the pal-

lid bat auditory system, the dominant patterned input to neurons involved in echolocation is likely to be downward FM sweeps. Consistent exposure to downward sweeps with a small range of FM rates may cause neurons to favor inputs that are co-activated with the spectrotemporal relationships of inhibition and excitation naturally present in those sweeps (Engert *et al.*, 2002). The slower FM sweep rates and the reduced high frequencies that the muted pups experience have a different spectrotemporal sequence compared to normal echolocation calls, and the coincident pre-synaptic events may not be driven by the same combination of inputs that drive neurons in the normal group. This would result in weakening of synapses established in an experience-independent manner and/or prevention of experience-dependent refinement.

The data on control pups raised in isolation show that self-produced vocalization is sufficient for normal development of echolocation call selectivity. However, these data do not address whether self-vocalizations are necessary. To address this, muted pups were placed back in the main colony where they heard the echolocation calls of flying bats during development. These pups showed the same deficit (in sweep selectivity and sideband inhibition) at P30 as muted and isolated pups (Razak and Fuzessery, unpublished observations) indicating that normal self-vocalizations are necessary. Future studies are needed to address the mechanisms through which sensorimotor interactions instruct development of sweep selectivity in cortical neurons.

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