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REVIEW

Multiple mechanisms shape selectivity for FM sweep rate and direction in the pallid bat inferior colliculus and auditory cortex

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Abstract The inferior colliculus and auditory cortex of the pallid bat contain a large percentage of neurons that are highly selective for the direction and rate of the downward frequency modulated (FM) sweep of the bat's echolocation pulse. Approximately 25% of neurons tuned to the echolocation pulse respond exclusively to downward FM sweeps. This review focuses on the finding that this selectivity is generated by multiple mechanisms that may act alone or in concert. In the inferior colliculus, selectivity for sweep rate is shaped by at least three mechanisms: shortpass or bandpass tuning for signal duration, delayed high-frequency inhibition that prevents responses to slow sweep rates, and asymmetrical facilitation that occurs only when two tones are presented at appropriate delays. When acting alone, the three mechanisms can produce essentially identical rate selectivity. Direction selectivity can be produced by two mechanisms: an early low-frequency inhibition that prevents responses to upward sweeps, and the same asymmetrical two-tone inhibition that shapes rate tuning. All mechanisms except duration tuning are also present in the auditory cortex. Discussion centers on whether these mechanisms are redundant or complementary.

Keywords Gleaning bats · FM sweep · Sweep rate selectivity · Sweep direction selectivity · Pallid bat

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Abbreviations

FM	frequency modulated
TTF	two-tone facilitation
DSI	direction selectivity index

Introduction

Gerhard Neuweiler, among his many significant accomplishments, was instrumental in advancing our understanding of the incredible diversity of life styles of bats, and the strategies they use to effectively exploit various ecological niches. While his greatest love may have been for the Rhinolophids and their acoustic foveae, the gleaners also engaged his curiosity. The gleaners are a functional group made up of species from several families that have converged upon the strategy of taking prey from substrates, as opposed to capturing flying insects. Gleaners rely heavily on the passive sound localization of prey-generated sounds to capture their prey, since prey are often embedded in "acoustic clutter" that can render echolocation difficult. However, other sensory modalities such as vision, echolocation, and olfaction may also be used, depending upon the foraging strategy of a given species.

The pallid bat (*Antrozous pallidus*), the subject of this review, appears to be particularly dependent upon passive sound localization, and is capable of 1°–2° angular resolution in response to a single, brief noise burst (Fuzessery et al. 1993; Barber et al. 2003). Its echolocation may be reserved mainly for obstacle avoidance. Therefore, while hunting, the pallid bat simultaneously attends to two streams of acoustic information. It is this need for effective "dual-stream" processing (Barber et al. 2003) that appears to have dictated the unusual organization of its central auditory system. It has evolved essentially two auditory systems that are functionally and anatomically segregated, at least from the levels of the inferior colliculus to auditory cortex. Where this segregation starts at lower levels of the auditory system remains to be examined.

At the level of inferior colliculus, an extreme lateral region typically occupied by the external nucleus in other species, contains neurons that respond preferentially to noise transients (Fuzessery 1997). They exhibit remarkable temporal acuity, responding to amplitude modulated noise at rates as high as 1,400 Hz. Their short response latencies and anatomical connections with the lower brainstem indicate that this lateral shell is a specialized region of the central nucleus of the inferior colliculus. Their acuity for relevant interaural time and intensity differences suggests that they may be dedicated to the passive sound localization of prey-generated noise transients (Fuzessery 1997). Interestingly, a comparable region in a distantly related megadermid gleaner also exhibits a similar sensitivity to noise transients (Rubsamen et al. 1998), suggesting a possible neuroanatomical convergence of function. Processing of the echolocation pulse, a downward FM sweep, occurs more medially in the deeper isofrequency layers of the inferior colliculus tuned to $\geq$30 kHz. Here approximately half of the neurons respond selectively to tones and downward FM sweeps. Around 25% respond only to downward FM sweeps (Fuzessery 1994). These highly selective spectrotemporal filters likely serve to allow responses only to sounds associated with echolocation.

Anatomical and functional segregation is similarly present in the auditory cortex. There is a rough tonotopy of low- to high-frequency representation in the caudorostral direction (Razak and Fuzessery 2002). Neurons tuned to $\leq$30 kHz respond preferentially to narrow- or broadband noise transients over single, pure tones, while those tuned to higher frequencies respond selectively to the downward FM sweep of the echolocation pulse. The rather crude tonotopy of the auditory cortex suggests that this system places an emphasis on the processing of prey-generated noise transients and echolocation, rather than frequency representation.

The sources of the thalamocortical inputs to these cortical regions are also anatomically segregated (Razak et al. 2007). Retrograde tracing revealed that input to the low-frequency, noise-selective region comes from the ventral division of the medial geniculate body. This is the typical primary auditory pathway seen in all mammals. However, projections to the high-frequency, FM-selective region originate with the dorsal medial geniculate body and predominately within the suprageniculate nucleus of this division. Thus the pallid bat presents an unusual case in which what appears to be primary auditory cortex, based upon tonotopy, gets discrete input from two divisions of the medial geniculate body, unlike the more typical mammalian condition in which primary auditory cortex is, in part, defined by the fact that it receives input from the ventral medial geniculate body.

The remainder of this review focuses on the mechanisms that create neuronal response selectivity for the sweep rate and direction of the pallid bat echolocation pulse at the level of the inferior colliculus and auditory cortex, and whether the auditory cortex inherits this selectivity or recreates it at the cortical level. This pulse sweeps downward from 60 to 30 kHz in 1.5–6 ms (Brown 1976). With a few exceptions, similar spectrotemporal filters and underlying mechanisms exist at the collicular and cortical level. To provide a brief background, FM sweeps are important and ubiquitous components of vocalizations. It is therefore not surprising that the neural mechanisms that process these spectrotemporally dynamic signals have received considerable attention for over four decades. As also noted in studies of direction selectivity in the visual system (e.g., Barlow and Levick 1964; Sillito 1977; Reid et al. 1991; Livingstone 1998), the fundamental requirement for direction selectivity across any sensory surface is some form of asymmetry that allows excitation in only one direction of motion. In the auditory system, this asymmetry has been modeled as the spatiotemporal integration of postsynaptic events (Rall 1959; Segev 1992; Softky 1994; Gulledge et al. 2005; Voytenko and Galazyuk 2007), as a result of interactions between networks of neurons (Suga 1965; Gordon and O'Neill 1998) and correlated with differential low- and high-frequency sideband inhibition (Britt and Starr 1976; Heil et al. 1992; Shannon-Hartman et al. 1992; Suga 1965; Zhang et al. 2003). The relative arrival times, bandwidths, and spectra of inhibitory and excitatory inputs can influence both sweep direction and rate selectivity (Gordon and O'Neill 1998; Fuzessery et al. 2006; Andoni et al. 2007; Fishbach et al. 2003). It has also been suggested that the precise timing of excitatory inputs and/or rebound from inhibition, occurring only during an FM sweep of given direction and rate, may coincide and summate to produce a response (Phillips et al. 1985; Casseday et al. 1997; Covey and Casseday 1999; Sanchez et al. 2008; Razak and Fuzessery 2008). Much of this research can be placed in two categories: spectral delay lines in which motion in one direction is excitatory, and either non-excitatory or inhibitory in the other, and asymmetrical sideband inhibition that suppresses a response in one direction, but not the other.

A significant contribution of the study of FM sweep selectivity in the pallid bat is the identification of four mechanisms that contribute to sweep direction or rate selectivity, or both. These are low- and high-frequency inhibitory sidebands, an early on–best frequency inhibition, and facilitation. More than one mechanism can shape the same form of selectivity and more than one mechanism can contribute to shaping sweep rate or direction selectivity.

Materials and methods

Methods used in these studies are provided in detail elsewhere (Fuzessery et al. 2006; Razak and Fuzessery 2008). Briefly, the bats were initially anesthetized with Metofane (methoxyflurane) inhalation, followed by an intraperitoneal injection of pentobarbital sodium (30 μg/kg body weight) and acepromazine (2 μg/kg body weight), which kept the bats lightly anesthetized during recording sessions. Bats were isolated in a heated, soundproofed chamber, and electrodes advanced remotely using a Kopf model 660 Micropositioner. Sounds were presented as closed-field stimuli through Infinity emit-K ribbon tweeters fitted with funnels that were inserted into the bat's pinnae and acoustically sealed in place with petroleum jelly. Extracellular recordings were made with glass microelectrodes filled with 1 M NaCl, with tip resistances of 3–7 MΩ. Stimuli were generated with Modular Instruments and Tucker Davis Technologies digital hardware, and controlled with custom software.

All neurons studied were tuned to frequencies within the spectrum (30–60 kHz) of the bat's echolocation pulse. Sounds were presented at the interstimulus intervals of 400 ms. For each neuron, all sounds were presented at a single intensity 5–20 dB above the response threshold. Data collection proceeded in the following sequence. If a neuron responded to tones, its excitatory tonal response area was mapped audiovisually as the combinations of sound pressure levels and tone frequencies evoking a response to each of 10 consecutive stimulus presentations. Responses to the signals were quantified as the total number of spikes elicited by 30 stimulus presentations.

Duration selectivity was tested at a neuron's best frequency. A neuron was considered duration selective if it exhibited a shortpass or bandpass duration function in which responses dropped to $\leq$50% of maximum response as tone duration increased or decreased relative to the best duration. The best duration was defined as the arithmetic center of the durations evoking a $\geq$80% maximum response. Duration tuning was defined only in response to tones, and not in response to FM sweeps, since response changes with FM sweep duration could be due to a selectivity for sweep rate, rather than sweep duration.

Responses to linear upward and downward FM sweeps of identical spectra were then tested to determine direction selectivity. The spectra of FM sweeps were centered on the neuron's best frequency. A neuron was termed selective for sweep direction if the maximum response in one direction had a directional selectivity index (DSI) of $\geq$0.6 (at which the response to the non-preferred direction was 25% of the response to the preferred direction). The DSI = $(D - U)/(D + U)$, where D and U are the maximum responses to downward and upward sweeps, respectively, regardless of the sweep rates at which they occurred. All direction-selective neurons preferred the downward direction; therefore, preference for this direction was assigned a positive value, unlike the convention used in previous studies.

Downward FM selective neurons were defined as responding similarly to both downward FM sweeps and tones, but giving $\leq$20% of maximum response to upward sweeps and noise. Downward FM specialists were more selective. They responded maximally only to downward sweeps, and gave $\leq$20% to tones, upward sweeps, and noise.

Bandpass noise with the same bandwidths as excitatory FM sweeps was presented as a control to determine whether a neuron actually required the orderly progression of frequencies present in a sweep, or whether the simultaneous presentation of a spectrum that encompassed both the excitatory and inhibitory tonal response areas was also excitatory.

Selectivity for FM sweep rate was then tested by presenting FM sweeps of at least three different bandwidths, centered on the neuron's best frequency and located, to the extent possible, within the bandwidth of bat's echolocation range of 25–80 kHz. Sweep rates were varied by holding bandwidth constant and changing sweep duration. Sweep rates were calculated by dividing the bandwidth by the duration (kHz/ms). The best sweep rate was calculated by taking the arithmetic center of $\geq$80% maximum response for each rate function, and averaging them.

The presence and extent of inhibitory sidebands were determined by presenting an excitatory tone at best frequency of shorter duration (1–5 ms) than a second tone outside of the excitatory tuning curve. The onset of the best frequency tone was varied with respect to the fixed onset of the second tone, and inhibitory regions were mapped audiovisually as a complete suppression of response to 10 consecutive stimulus presentations. The frequency of the second tone was then varied to map the extent of the inhibitory sideband. The result was a plot of two-tone inhibitory fields over time. If the onset of the excitatory tone was advanced relative to that of the inhibitory tone, and the response could still be suppressed, then inhibitory input was assumed to arrive before excitation. If the excitatory tone had to be delayed before the second tone suppressed the response, then it was assumed that excitatory input arrived before inhibition. The role of two-tone facilitation (TTF) in shaping sweep rate and direction selectivity was tested only in FM specialist neurons that responded solely to downward FM sweeps, since neurons that also responded to tones seldom increased response in the presence of two tones. Tone pairs (1 ms, 0.5 ms rise/fall time) near the center of the excitatory region (5–10 dB above threshold for response to FM sweeps) were used to characterize facilitatory responses that might occur during the course of an FM sweep. Facilitation was defined as a response to two tones that was greater than the sum of responses to each individual tone. The time delay between presentation of the first and second tone was varied to characterize any preference for presentation of either the low- or high-frequency tone first, and the optimal time delay between the tones. The TTF data were used to predict the best sweep rates. These sweep rates were calculated from the TTF data as the spectral difference between tones (kHz) divided by the delay (ms) between tones.

Results

Here we review the mechanisms that shape sweep rate and direction selectivity, comparing them at the levels of the inferior colliculus and auditory cortex. The roles of duration tuning and high- and low-frequency inhibitory sidebands were studied only in neurons that responded to both FM sweeps and tones (Fuzessery et al. 2006; Razak and Fuzessery 2006). In the inferior colliculus, 42 of 64 (66%) neurons studied were selective for downward sweeps, and none were selective for upward sweeps. 30 of the 42 neurons (71%) responded to both sweeps and tones. Fastpass or bandpass sweep rate selectivity was observed in 35 of 40 (88%) neurons tested, with best rates ranging from 1 to 13 kHz/ms (average 3.9 kHz/ms). Similar results were obtained in the auditory cortex. 31 of 51 (61%) neurons were selective for downward sweeps, and none were selective for upward sweeps. 46 of 61 (75%) neurons tested were fastpass or bandpass selective for sweep rates, with best rates in 92% falling between 2 and 5 kHz/ms.

Duration tuning and sweep rate tuning

The most significant difference between the inferior colliculus and auditory cortex is that, while around 60% of inferior colliculus neurons tuned to the echolocation pulse spectrum are shortpass or bandpass selective for durations of <5 ms (Fuzessery and Hall 1999), these forms of duration tuning are absent in the auditory cortex (Razak and Fuzessery 2006).

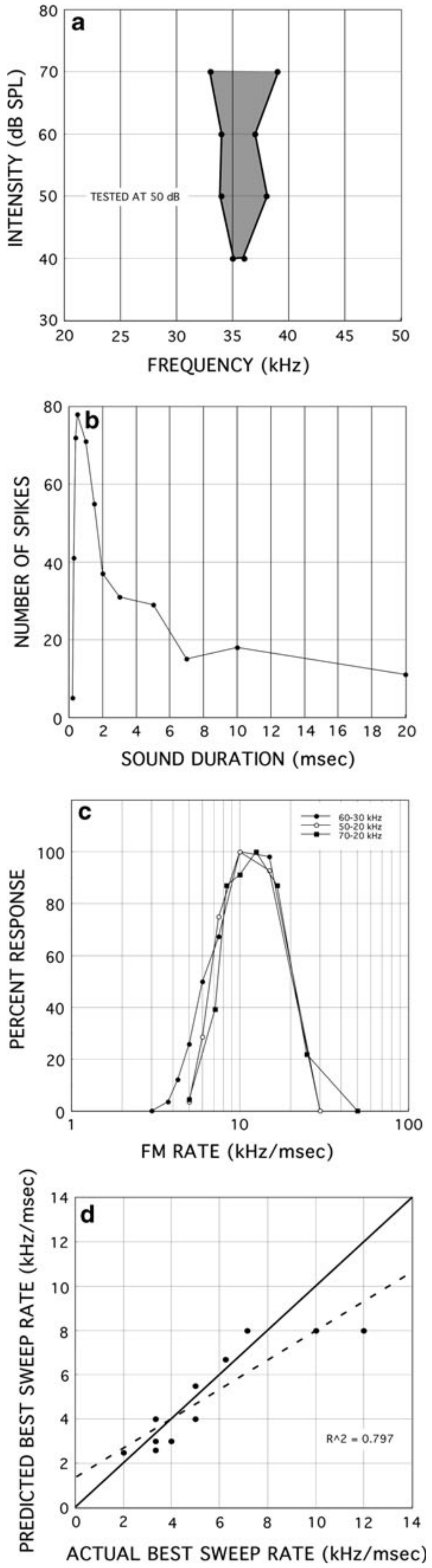
Duration tuning for tones has been suggested (Fuzessery and Hall 1999) to result from an early on–best frequency inhibition that lasts the duration of a sound. If the sound is long enough, then this inhibition will overlap with a later, fixed-latency excitatory input, and suppress the response. If a neuron is duration tuned, it will also show fastpass or bandpass sweep rate selectivity. The assumption is that a neuron will prefer a sweep rate in which the time spent within its excitatory tuning curve is equal to the best duration. The predicted best rate of a neuron is therefore the excitatory bandwidth divided by the best duration. An example is shown in Fig. 1. The excitatory bandwidth (Fig. 1a) is 4 kHz at the test intensity (50 dB), and best duration is 0.5 ms (Fig. 1b), leading to a predicted best rate of 8 kHz/ms. The actual best rate is 12 kHz/ms (Fig. 1c). Figure 1d summarizes the predicted and actual best rates for 11 neurons. This high correlation ($r^2 = 0.797$) suggests that duration tuning contributes to rate tuning in these neurons.

Fig. 1 The information used to predict the best FM sweep rate of a duration-tuned neuron in the inferior colliculus, by the formula of rate = kHz/ms = excitatory bandwidth/best duration. **a** The bandwidth of the excitatory tuning curve at the test intensity of 50 dB is 4 kHz. **b** The best duration of the neuron is 0.5 ms. The predicted best rate is therefore 4/0.5 = 8 kHz/ms. **c** The actual best rate of this neuron, tested with three downward FM sweeps of different bandwidth, is 12 kHz. **d** The actual and predicted best FM sweep rates for downward FM sweeps of 11 neurons with duration tuning. The *solid diagonal line* indicates a perfect prediction; the *dashed line* is a simple linear regression. The r^2 value is 0.797 ▶

Inhibitory sidebands

Two properties of sideband inhibition contribute to a neuron's sweep rate and direction selectivity: the arrival time of inhibition relative to excitation, and the bandwidth of the inhibitory flank. The earlier the arrival time of inhibitory input driven by frequencies within the sideband, the more likely it will suppress responses to FM sweeps entering the sideband before arriving at the excitatory tuning curve. Likewise, the broader the bandwidth of the inhibitory sideband, the earlier the inhibitory input will be triggered, and the more likely it will suppress the response.

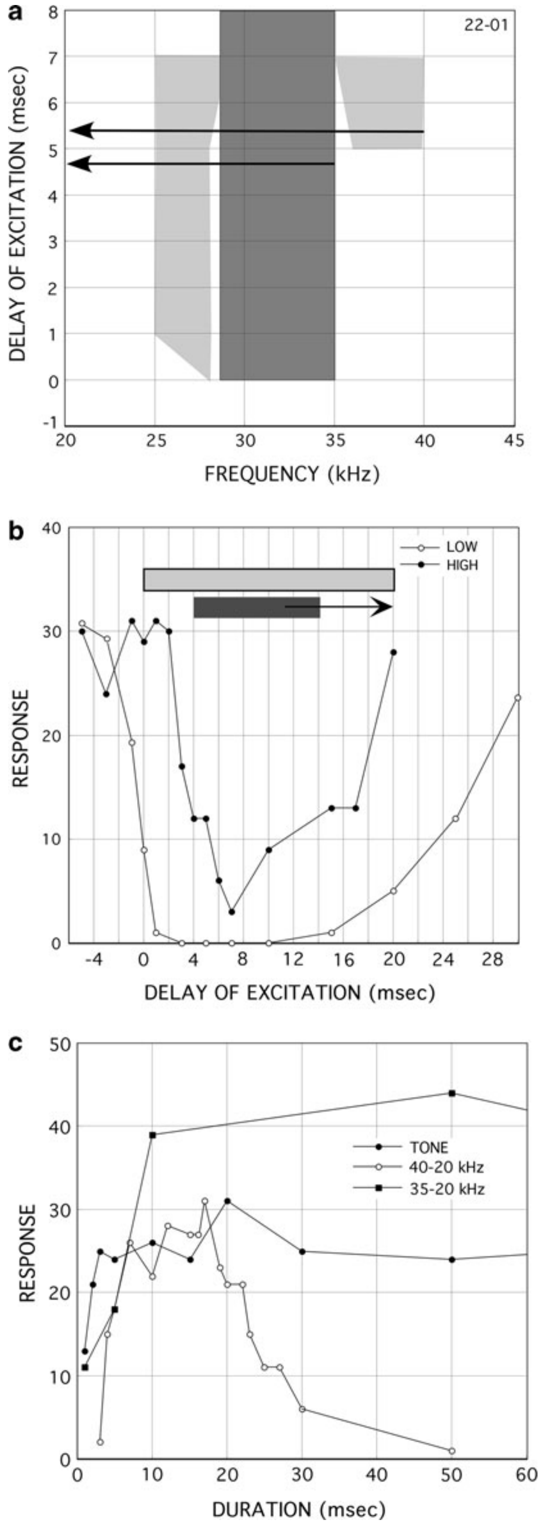
When these two properties are compared in low-frequency (lower than excitatory frequencies) and high-frequency inhibition (higher than excitatory frequencies), they are significantly different in both the inferior colliculus and auditory cortex. An example from the inferior colliculus is shown in Fig. 2. In 36 inferior colliculus neurons tested, all had low-frequency inhibition, but only 22 had high-frequency inhibition. The average arrival times for low- and high-frequency inhibition were 0 ms and 2.37 ms, respectively, with the positive value indicating it arrived later than excitation. The average bandwidths for low- and high-frequency inhibition were 15.0 and 4.2 kHz, respectively. Similar differences in arrival times (−0.37 ms low and 3.35 ms high) and bandwidths (8 kHz low and 4 kHz high) were also found in the auditory cortex.



Low-frequency inhibition arrives earlier than high-frequency inhibition, and its sideband bandwidth is broader. It follows that low-frequency inhibition will likely create selectivity for the downward sweep direction by suppressing responses to upward sweeps that must traverse the sideband before triggering excitatory input. This was tested in two ways: correlating selectivity for downward sweeps with the arrival time of low-frequency input, and eliminating low-frequency inhibition from upward sweeps and assessing the change in direction selectivity. Figure 3a shows a summary of auditory cortex neurons relating their DSIs to the arrival time of low-frequency inhibition. There is a general trend in which neurons with early arrival times have a greater selectivity for downward sweeps (positive DSI values). Low-frequency inhibition was eliminated from upward FM sweeps by starting the sweeps at the low-frequency side of the excitatory tuning curve. In the auditory cortex, of 33 neurons tested that were selective for downward sweeps, all became responsive to upward sweeps following this manipulation of the sweep spectrum. Similarly, in the inferior colliculus, of the 12 neurons tested, 10 became responsive to upward sweeps. It is not clear why the other two neurons remained selective for downward sweeps; other undetermined mechanisms may contribute to their selectivity.

It is worth mentioning one unusual inferior colliculus neuron to illustrate a point. This neuron had the earliest arriving low-frequency inhibition observed of −3 ms. It did not respond to FM sweeps in either direction, apparently because even though a downward sweep would encounter the low-frequency sideband after it traversed the excitatory tuning curve, the low-frequency inhibition arrived early enough to still suppress the response. As expected, if the low-frequency sideband spectrum was excluded from a downward sweep, the neuron then responded. The point to be emphasized here is that the low-frequency inhibition must arrive within a narrow, millisecond time window to be effective in creating direction selectivity. If it were to arrive too early, responses to both upward and downward FM sweeps would be suppressed. If it arrives too late, direction selectivity is lost.

High-frequency inhibition arrives late relative to excitation, and its inhibitory bandwidth is narrow relative to low-frequency inhibition. High-frequency inhibition serves to create fastpass or bandpass rate selectivity for downward sweeps, the assumption being that fast downward sweeps traverse this sideband rapidly enough to trigger excitatory input before the delayed high-frequency inhibition arrives. As sweep rate slows, the inhibition catches up and arrives earlier than excitation, and the response is therefore suppressed. The role of high-frequency inhibition in shaping



◀ **Fig. 2** **a** A “two-tone inhibition over time” function of an inferior colliculus neuron showing the excitatory tuning curve (*dark gray*) and flanking inhibitory sidebands (*light gray*) as a function of frequency tuning and arrival time of inputs relative to excitation. The low-frequency inhibitory inputs arrive at the same time as excitation, while the high-frequency inhibitory input arrives 5 ms later. The *arrows* indicate two downward sweeps, one including the high-frequency sideband, the other eliminating it. **b** A two-tone inhibition analysis of the arrival times of low- and high-frequency inhibition. An excitatory tone is delayed and advanced with respect to a tone from each band. Note that the low-frequency tone suppresses the response much earlier (1 ms delay of the excitatory tone) than the high frequency. **c** The effect of eliminating the high-frequency inhibitory sideband from a downward sweep on rate selectivity. Rate selectivity is eliminated, since the neuron now responds at all sweep durations, and hence rates

rate tuning was tested in two ways. The first was to predict the downward sweep rate at which the response would be suppressed. This is the bandwidth of the inhibitory flank (kHz) divided by the arrival time (ms) of inhibition, which is the “cutoff rate” (kHz/ms) at which the response is suppressed. A summary of the actual and predicted cutoff rates from inferior colliculus data is shown in Fig. 3b. Similar predictive results were obtained from the auditory cortex.

The second method was to eliminate the high-frequency inhibitory flank. An example from the inferior colliculus is shown in Fig. 2. Note that when the downward sweep was started at 35 kHz (Fig. 2a), the neuron lost rate selectivity (Fig. 2c). It is important to also note that this neuron was not selective for tone duration (Fig. 2c), since duration selectivity can also create rate selectivity. Thus, for this neuron, it appears that only high-frequency inhibition shaped rate selectivity. In the auditory cortex, of 36 rate-tuned neurons tested in this fashion, all lost rate selectivity, suggesting that this is the only mechanism shaping this selectivity. In the inferior colliculus, all rate-selective neurons that were duration tuned did not lose rate tuning when high-frequency inhibition was eliminated. However, eight neurons that were not duration tuned were tested in this fashion, and seven lost their rate selectivity. Thus, in the inferior colliculus, two mechanisms create rate selectivity in these neurons, while only one mechanism operates at the cortical level.

Facilitation

The role of facilitation in shaping both sweep rate and direction selectivity was tested only in FM specialists which respond to downward sweeps, but not to single tones within the sweeps. It is this lack of response to tones that allowed testing for the presence of TTF. Similar results were obtained in the inferior colliculus and auditory cortex. In the inferior colliculus, approximately 25% of neurons tuned to the echolocation pulse are FM specialists. Of 58 FM specialists tested in the IC, 87% were selective for downward sweeps; the remainder had no direction preference. Of 33 neurons tested, 78% were also fastpass or bandpass selective for downward sweep rates. The main finding is that, in both inferior colliculus and auditory

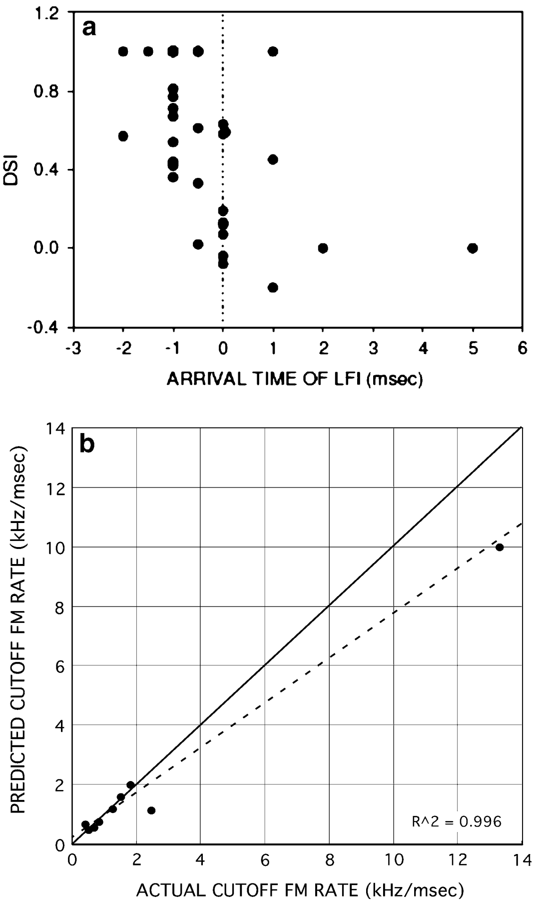


Fig. 3 **a** The arrival time of low-frequency inhibition (LFI) predicts direction selectivity in auditory cortex neurons. *Vertical dashed line* indicates when excitatory and inhibitory inputs arrive at the same time. Negative values mean inhibition arrives earlier. Most neurons with early inhibition have higher direction selectivity. **b** The actual and predicted cutoff rates of nine inferior colliculus neurons, predicting the fastest rate at which their response would be reduced by 90% of maximum response. Rate tuning is assumed to be shaped by delayed high-frequency inhibition. *Solid line* indicates a perfect prediction. The *dashed line* shows a linear regression with an r^2 value of 0.996

cortex, facilitation alone is capable of creating both rate and direction selectivity. This assertion was tested by showing that the rate selectivity could be predicted from TTF functions (not shown, best rate = spectral difference between tones/delay evoking maximum response), and showing that direction and rate selectivity remained even when FM sweeps were limited to the narrow bandwidths over which facilitation occurred.

An example of an FM specialist from the inferior colliculus exhibiting asymmetrical TTF is shown in Fig. 4. When two 1 ms tones narrowly separated in frequency (38 and 40 kHz) were presented at small delays, facilitation occurred only when the higher frequency tone preceded, as would occur in a downward sweep (Fig. 4a). This process was then repeated with different pairs of tones to construct an “FM tuning curve” that ranged from approximately 38 to 40 kHz (Fig. 4a). This neuron responded only to downward broadband sweeps and exhibited bandpass rate selectivity (Fig. 4b). Similarly, it also responded to narrowband sweeps within the FM tuning curve (Fig. 4a). When frequencies higher or lower than the FM tuning curve were eliminated from these sweeps (Fig. 4a,b), direction and rate selectivity remained, indicating that the frequencies outside of the FM tuning curve (that were possibly inhibitory sidebands) were not needed to shape this neuron’s selectivity. Across the population, 15 inferior colliculus neurons that showed strong asymmetrical facilitation tended to show less loss of direction selectivity when frequencies below the FM tuning curve were eliminated, indicating that facilitation played a significant role in shaping this selectivity. In contrast, neurons that did not show asymmetrical facilitation were more likely to lose this selectivity, suggesting that frequencies outside of the FM tuning curve played an important role.

Discussion

There are several fundamental conclusions that can be drawn from this review of the mechanisms that shape selectivity for FM sweep rate and direction. At the inferior colliculus level, at least four mechanisms are in place to shape the required spectrotemporal filters. Two mechanisms, early low-frequency inhibitory sidebands and asymmetrical facilitation, shape selectivity for the downward sweep direction. The first prevents a response to upward sweeps, while the second is produced only in the downward sweep direction, suggesting that these may be discrete, complementary mechanisms. Three mechanisms, duration tuning, delayed high-frequency inhibition and asymmetrical facilitation, shape selectivity for the rate of a downward sweep. Duration tuning for tones is due to an early, on–best frequency inhibition; it also endows a neuron with sweep rate selectivity. Delayed high-frequency inhibition is obviously off-best frequency, and prevents a response to slower sweep rates. Asymmetrical facilitation occurs only when two tones in the correct sequence are presented at delays similar to those that are present in a downward sweep. Again, these mechanisms appear to occur under different spectrotemporal conditions and/or at different frequencies within a neuron’s receptive field, suggesting that they may be discrete mechanisms. A counter argument is that these mechanisms combine to produce complex spectrotemporal receptive fields whose origins in multilevel circuitry and synaptic interactions remain poorly understood. There may be more commonality among these mechanisms than is currently apparent.

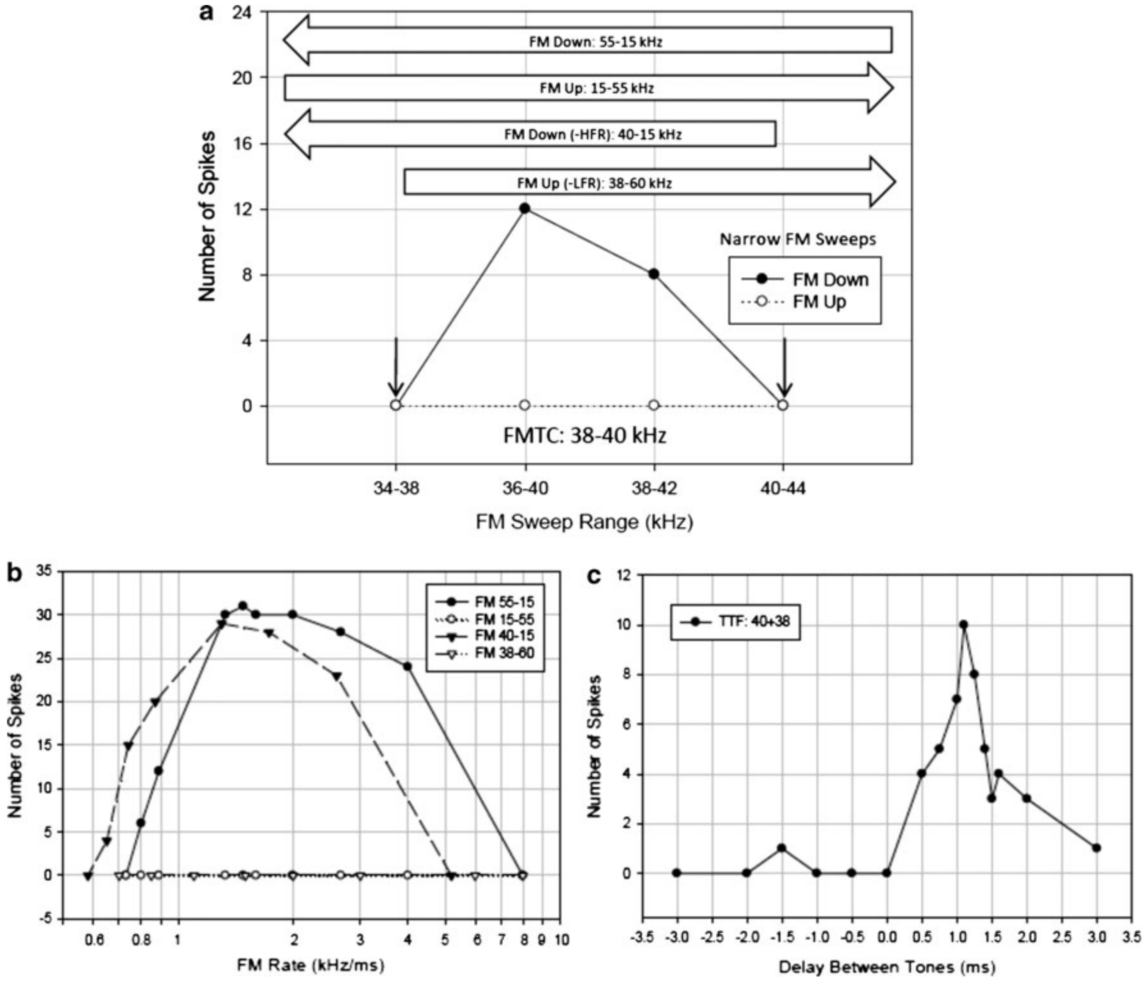


Fig. 4 Facilitation alone may shape sweep direction and rate selectivity in this inferior colliculus neuron. **a** Tests used to eliminate sideband inhibition, which also shapes response selectivity. This neuron was selective for downward sweeps. The FM tuning curve (FMTC) ranged from 38 to 40 kHz. Possible inhibitory sidebands were eliminated by starting upward (38 → 60 kHz) and downward (40 → 15 kHz) sweeps within this tuning curve. **b** The neuron retained its direction and rate selectivity for downward sweeps when both broad- and narrowband sweeps were presented, suggesting that inhibitory sidebands did not contribute to response selectivity. **c** The neuron had a strongly asymmetrical TTF that may shape both direction and rate selectivity. HFR is high-frequency region; LFR is low-frequency region

These mechanisms can act alone or in concert to shape response selectivity, and when acting alone, can generate identical forms of sweep direction and rate selectivity. Their properties appear remarkably robust and linear, in that a few algebraic relationships can be used to determine how tones predict responses to a more spectrotemporally complex sound (i.e., FM sweeps). Are these mechanisms redundant or complementary? If one accepts the hypothesis that the pallid bat, or gleaners in general, benefit greatly from being able to effectively separate the processing of echolocation and passive hearing, then one might argue that natural selection has provided redundant mechanisms to subserve echolocation processing. However, this may be an oversimplification. Only selectivity for FM sweep parameters has been studied; these various mechanisms may also serve in the selective detection of other aspects of echolocation.

Analysis at two levels of the system permits speculation on whether, if a form of selectivity is present at a lower level, a higher level simply inherits what as been created. Neurons in the auditory cortex do not exhibit the duration tuning present in the inferior colliculus, where it shapes rate selectivity in about 50% of the neurons that exhibit this property. Sweep rate selectivity in auditory cortex neurons is created only by high-frequency inhibition or asymmetrical facilitation, since they do not inherit duration tuning. This suggests that the auditory cortex may need to create or fine-tune sweep rate selectivity. In support of this hypothesis, blocking GABAa receptors in the pallid bat auditory cortex does reduce or eliminate rate and direction selectivity (Razak and Fuzessery 2009). Similar results have been reported in the mouse auditory cortex (Zhang et al. 2003). While perhaps counterintuitive and seemingly inefficient, this issue deserves more attention.

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