TEMPORAL TUNING FOR FM SWEEPS IN THE INFERIOR COLLICULUS

TUNING FOR THE RATE AND DURATION OF FREQUENCY MODULATED SWEEPS IN THE INFERIOR COLLICULUS OF THE BIG BROWN BAT

By: JAMES MORRISON, B.Sc.

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AUTHOR: James Morrison, B. Sc. (McMaster University)

SUPERVISOR: Professor Paul A. Faure

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**Biography**

I was born on October 29th, 1990 to Warren and Janette Morrison. My fascination with science began at a very early age, as my grandmother can recall when I would flip my stroller on its side and spin the wheels at different angles to see how the rotation changed. I went to elementary school at Algonquin Ridge Elementary School in Barrie, and then went to high school at Innisdale Secondary School. I particularly enjoyed physics in high school. This was likely due to my wonderful instructor, Mr. Mitchinson, though his methods were somewhat unorthodox. For example, our main assignment for the kinematics module was to launch a ball from an automated slingshot onto a lunch tray. We were given all the required information about launch speed, angle, etc, and were required to calculate where the ball would land and position the tray accordingly. We were given three launch attempts and only once we hit the tray were we able to submit our assignments for marking. My enjoyment of physics pushed me to apply for undergraduate engineering programs, and in 2008 I was accepted into my first choice program at McMaster University.

I enjoyed first year engineering, which as my peers described was just “science on hard mode”. Once I entered second year and my courses became more specialized, my interest in engineering began to dwindle. I asked my friends in the program if they had similar concerns and once I realized that I was the only one, I decided it was time to make a switch. After surveying all the programs McMaster had to offer, I chose the most interesting one I could find: Psychology, Neuroscience & Behaviour. I joined several labs for research projects and found myself enamoured with the academic research culture. I completed an undergraduate thesis and after graduating, enrolled in a Master’s degree.

As for what’s next, I am currently enrolled in the DeGroote MBA program at McMaster. I think the program has a perfect blend of analytical and psychological thinking for me. As such, I plan to pursue co-op positions in either finance or marketing for my first two terms and decide which I like better for the third. After that I plan to settle down and start a family as soon as my girlfriend decides she can put up with me for that long.

**Abstract**

I investigated how the auditory system encodes frequency modulated (FM) sweeps, by recording neuronal responses in the auditory midbrain (inferior colliculus, IC) of the big brown bat, (*Eptesicus fuscus*) while searching for the responses of so-called “FM duration-tuned neurons (DTNs)”. The responses of DTNs are selective for stimulus duration. My project investigated how the responses of FM DTNs encode the two temporal properties of FM sweeps: sweep duration, and the rate of frequency change (i.e. sweep rate). Based on previous studies, it was unclear whether FM DTNs were tuned to signal duration like classic DTNs, or simply the rate of FM. I addressed this question using single unit extracellular recordings from DTNs in the IC of *E. fuscus*. First, I measured the spectral tuning parameters of a cell, and then FM pulses were randomly varied in duration to measure the temporal bandwidth of duration tuning of the cell. To separate FM rate tuning from duration tuning, the duration tuning of the cells was tested at different sweep bandwidths (i.e. doubled or halved) while keeping the center frequency constant. If a neuron is tuned to stimulus duration, then the range of excitatory signal duration(s) should not change with changes in FM bandwidth; however, if the cell is tuned to the rate of FM, then the range of excitatory durations should corresponed to the same FM rate of each altered bandwidth. A Bayesian model comparison showed that an overwhelming majority of FM DTNs were in fact tuned to sweep rate. Thus, I conclude that the dominant response parameter for temporal tuning of FM cells in the IC of the bat is not signal duration, but FM sweep rate.

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Thank you Paul Faure for collecting pilot data for this study during his postdoctoral fellowship in Ellen Covey’s laboratory at the University of Washington and Niki Efantis for assistance with data organization. Thank you Dr Daniel Goldreich for assisting with the creation of the Bayesian models used to analyze the data. It would have been a nearly impossible task for me to properly complete this on my own. Finally, thank you Brandon Aubie for developing SpikeDB, a custom software program for analyzing SPIKE files. It is so useful that the current generation of electrophysiology students is almost entirely dependent on it.

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**Abbreviations**

AM Amplitude modulated (modulation)

BD Best Duration

BF Bayes Factor

BR Best Frequency Modulated Sweep Rate

BW Stimulus Frequency Modulation Bandwidth

CEF Center Frequency

dB Decibel

DTN Duration Tuned Neuron

EPSP Excitatory Post-Synaptic Potential

eRA Excitatory Response Area

FM Frequency modulated (modulation)

IC Inferior Colliculus

IPSP Inhibitory Post-Synaptic Potential

iRA Inhibitory Response Area

SBW Best Frequency Modulated Sweep Bandwidth

SPL Sound Pressure Level

**Introduction**

Frequency modulation (FM) is present in the vocalizations of many animals and neural tuning for FM is found across mammalian species (bats, Suga, 1965; cats, Mendelson & Cynader, 1985; rats, Gaese & Ostwald, 1995; primates, Liang et al., 2002). Humans are no exception as verbal communication involves broad usage of FM sounds on both cognitive (i.e. on the order of seconds) and perceptual (i.e. on the order of milliseconds) timescales. From our own experience, we know that spectral inflection of a sentence can change meaning without altering semantic content: upward inflection in frequency indicates a question, while downward inflection instead indicates a declarative statement. On shorter timescales, transitions between phonemes and sometimes the phonemes themselves involve an upward or downward modulation in frequency, an acoustic element termed a FM sweep (Liberman et al., 1967, Shannon et al., 1995, Doupe & Kuhl, 1999). These spectral changes are also accompanied by amplitude modulations (AM) in human speech, raising the possibility that the auditory system uses both cues to encode information. This was investigated by Nie et al. (2005) who investigated how speech perception can be enhanced by adding an FM processing component to the traditional AM processor in cochlear implants. They found that sentence recognition in a quiet environment was similar for both AM and AM+FM encoding implants, but that the AM+FM implants dramatically improved sentence recognition in the presence of ambient noise or competing voices. This result suggests that FM processing is a robust cue for speech perception and discovering how the central auditory system processes FM may be useful for treating hearing deficits in the future. With this thesis, I will be using the big brown bat (*Eptesicus fuscus*) as an animal model to investigate FM processing in the mammalian inferior colliculus (IC), focusing specifically on neural mechanisms underlying temporal selectivity of FM sweeps in the auditory midbrain.

The physiology of FM selective neurons in echolocating bats was first described by Suga (1964). Beyond the typical spectral and amplitude selectivity seen in most auditory neurons, selectivity for FM sweeps is also based on the direction of modulation (i.e. sweeping upward or downward in frequency) and is created by inhibitory sidebands (Suga, 1965). Suga (1965) described neurons as having an excitatory response area (eRA) spanning a certain spectral bandwidth, with any suprathreshold sound stimulus with frequencies in this eRA evoking action potentials, regardless of FM sweep direction. This eRA is flanked by inhibitory response areas (iRAs), and FM sweeps starting from these iRAs will not evoke action potentials. Suga (1965) hypothesized that neural selectivity for directionality would arise through different combinations of these iRAs. For example, neurons selective for downward FM sweeps would have predominantly low frequency inhibitory sidebands. Sounds starting at a low frequency and sweeping upward would evoke inhibition before excitation, preventing the neuron from spiking. On the other hand, downward sweeps would start at a high frequency where there is little to no inhibition, and thus the FM sweep would evoke excitation, and if suprathreshold, spiking before the onset of inhibition evoked by lower frequencies in the signal.

This idea was a good one and it led to the current findings which suggest that selectivity for sweep direction is created through a mechanism similar to how directional selectivity is created in the tactile (Costanzo & Gardner, 1980) and visual (Barlow & Levick, 1964, Sillito, 1977) modalities: asymmetric amounts of neural excitation and inhibition are generated for a FM sweep in one direction but not the other (Fuzessery et al., 2006). Recent studies have shown that FM selectivity may not be created *de novo* for some IC neurons and is instead being inherited from lower brainstem nuclei such as the nucleus of the lateral lemniscus and the superior olivary complex (Gittelman et al., 2009, Pollak et al., 2011). Although the mechanisms that create auditory FM directional selectivity have been extensively researched, what is less clear are the mechanisms that create temporal tuning (i.e. selectivity) in FM sweep neurons.

Temporal processing has been suggested to play an important role in the auditory system (Capranica, 1992) and duration tuned neurons (DTNs) are well documented at and above the level of the auditory midbrain in many species (e.g. frogs, Potter, 1965; bats, Jen & Schlegel, 1982, Pinheiro et al., 1991, Fuzessery & Hall, 1999, Mora & Kössl, 2004, Luo et al., 2008; rodents, Brand et al., 2000, Wang et al., 2006, Perez-Gonzalez et al., 2006). These cells are typically classified based on their temporal tuning response characteristics. A bandpass DTN responds maximally to some best duration (BD) stimulus with excitatory responses decreasing to ≤50% of maximum spike count for sounds both longer and shorter than BD. A shortpass DTN also has a BD but its excitatory responses only decrease ≤50% of the maximum spike count for sounds that are longer than the BD (for review, see Sayegh et al., 2011). Currently, the majority of reports investigating neurophysiology of duration tuning stimulated the cells using pure tones (e.g. Casseday et al., 1994, Ehrlich et al., 1997, Mora & Kössl, 2004, Luo et al., 2008, Aubie et al., 2009, Aubie et al., 2012) with much less known about the physiology of DTNs in response to FM sweeps. This is of interest because when DTNs are stimulated with FM signals there is an additional temporal parameter that the neurons could be selective for: the FM sweep rate or change in frequency per unit of time. Sweep rate tuning would certainly be advantageous for an echolocating mammal like *E. fuscus*, which primarily emits downward FM sweeps while hunting insect prey. During its approach to a flying insect, the bat increases the bandwidth of downward FM sweeps (e.g. from ~5 🡪 40 kHz) while shortening the duration of its biosonar calls from ≥10 ms down to ≤1 ms in the terminal phase (Simmons et al., 1979, Surlykke & Moss, 2000). The FM sweep rate changes dramatically from the approach to terminal phase of hunting. Rate tuning in FM neurons has been extensively reported in the pallid bat, *Antrozous pallidus*, but there are relatively few reports describing the temporal response properties of FM neurons in *E. fuscus*.

Neurons with temporal selectivity for FM sweeps have been reported in the IC of *E. fuscus,* (Ehrlich et al., 1997); however, it was unclear whether the reported ‘FM DTNs’ were truly tuned to the FM pulse duration or the FM sweep rate as described above. The goal of this study was to investigate the temporal tuning properties of the so-called FM DTNs to determine if these cells are selective for FM sweep duration or FM sweep rate. To do this single unit extracellular recordings were obtained from FM duration-selective units in the mammalian auditory midbrain. Upon isolating a unit, each cell’s frequency tuning characteristics were determined by presenting downward FM pulses to find the center frequency and FM bandwidth evoking the greatest spiking response. With these spectral parameters, FM pulses were varied in duration to determine the BD and range of excitatory durations for the cell. To distinguish duration tuning from sweep rate tuning, FM pulses were varied over the same range of durations but with the FM bandwidth altered (doubled or halved re: maximal FM response) while keeping the center frequency constant. This allowed for manipulation of the FM sweep rate without changing the pulse duration (i.e. a wider FM bandwidth yields a faster sweep rate for some signal duration). If the neuron is tuned to FM sweep duration, then the range of excitatory signal durations should not vary with changes in signal bandwidth; however, if the neuron is tuned to FM sweep rate, then altering the bandwidth should change the range of excitatory signal durations for the cell with wider bandwidths evoking spikes at longer durations and narrower bandwidths evoking spikes at shorter durations.

**2. Methods**

**2.1 Electrophysiological recordings**

The data for this study were collected at two laboratories -- one at the University of Washington (UW) and the other at McMaster University (MU). Procedures conducted in Seattle were approved by the UW’s Laboratory Animal Care and Use Committee. Procedures conducted in Hamilton were approved by the MU Animal Research Ethics Board and were in accordance with the Canadian Council on Animal Care. All data analyses were performed at MU. Prior to recording, animals in both locations were housed in an outdoor husbandry facility where the lighting and temperature were varied with ambient conditions. Water and food were available *ad libitum*.

*2.1.1 Surgical preparation*

Electrophysiological recordings were obtained from the IC of 25 awake big brown bats *Eptesicus fuscus* (13 from UW, 5 males 8 females; 11 from MU, 4 males, 7 females). Bats were brought into the laboratory 1-3 days prior to surgery to allow them to acclimatize. Bats were anesthetized either by a combination of Metofane (methoxyflurane) inhalation (1-5 min) and a subcutaneous injection of a neuroleptic (0.3 mL 1:1 mixture of 0.025 mg/mL fentanyl citrate + 1.25 mg/mL Inapsine (droperidol); 19.1 mg/kg), or by isoflurane:oxygen inhalation (mixture 1-5%; flow 1-5 L/min). Anesthetized bats were then placed in a foam-lined restraint, molded to the shape of the body to hold the bat firmly yet comfortably while still allowing access to the head. Bats in the restrainer were placed into a stereotaxic alignment system and a custom bite bar/gas mask for isoflurane inhalation (David Kopf Instruments: Model 1900). The hair covering the skull was shaved and the underlying skin was swabbed with 70-100% ethanol followed by Betadine disinfectant. Local anesthetic (0.2 mL bupivicaine; 5 mg/mL) was injected subcutaneously prior to making a midline incision in the scalp. The temporal muscles were reflected, the skull was scraped clean and swabbed with 70-100% ethanol, and a stainless steel post was affixed to the skull to ensure that the position of the bat's head could be precisely replicated between recording sessions. The post was glued to the skull overlying the dorsal surface of the cortex with cyanoacrylate gel adhesive (Zap Gel, Pacer Technology) or superglue (Henkel Lockite Corporation) and instantly cured with liquid acrylic hardener (Jet Liquid, Lang Dental Mfg. Co.). One end of a chlorided silver wire attached to the head post was placed under the temporal musculature and served as the reference electrode.

*2.1.2 Stimulus generation*

Sound pulses were digitally synthesized with custom software controlling two signal processing boards from Tucker Davis Technologies (TDT: Apos II sampling rate = 357 kHz) that were optically interfaced to two digital-to-analog (D/A) converters (TDT: DA3-2). The output of each D/A was fed through a lowpass anti-aliasing filter (TDT FT6-2; fc = 120 kHz) and one (TDT PA5; MU) or two programmable attenuators (TDT PA4; UW) before being mixed in a summer with equal weighting (TDT SM5) and fed through a manual attenuator (Leader LAT-45) prior to final amplification (Krohn-Hite Model 7500). All stimuli were presented monaurally, contralateral to the IC being recorded, with a Brüel & Kjær (B&K) 1/4 inch condenser microphone (Type 4939; protective grid on) modified for use as a loudspeaker with a transmitting adaptor (B&K Type UA-9020) to correct for nonlinearities in the transfer function (Frederiksen, 1977). The diaphragm of the loudspeaker was positioned ca. 1 mm in front of the external auditory meatus. The output of the speaker, recorded with a B&K Type 4138 1/8 inch condenser microphone (90° incidence; grid off) connected to a measuring amplifier (B&K Type 2606) and bandpass filter (Krohn-Hite Model 3500), was calibrated (B&K Type 4231) and expressed in decibels sound pressure level (dB SPL re 20 µPa) equivalent to the peak amplitude of continuous tones of the same frequency (Stapells, 1982). The loudspeaker transfer function was flat ±6 dB from 28 to 118 kHz, and there was at least 30 dB attenuation at the ear opposite the source (Ehrlich et al. 1997). All stimuli had rise/fall times of 0.4 or 0.5 ms shaped with a square cosine function, and were presented at a rate of 3 Hz.

**2.2 Single unit recording**

Single units were found by searching with short duration (2-10 ms), downward, linear, FM sweeps. Upon isolating a unit, the acoustic threshold (dB SPL), center frequency (CEF, kHz), and stimulus BD (ms) were measured. Acoustic testing was conducted in blocks consisting of 10-20 stimulus repetitions per variable step. Once a cell’s acoustic threshold was determined, all measurements were made at +10 dB above threshold. To minimize the effects of any spontaneous activity, the data were windowed so that spikes were only counted if they were evoked between stimulus onset and 50 ms after stimulus offset. Data analysis was automated using custom Matlab and Python scripts.

*2.2.1 Measuring response parameters*

Spectral tuning was measured with BD pulses varying in 1 kHz steps. Temporal tuning was measured with CEF pulses varying in 0.5-1 ms steps. The CEF of each cell was defined as the center frequency of the FM sweep stimulus with the lowest acoustic threshold. The BD was defined as the stimulus duration that evoked the greatest spike count at +10 dB above threshold using a CEF pulse. The best sweep bandwidth was measured using CEF BD FM pulses varying in bandwidth. To remove classic pure tone DTNs from the population, a cell was excluded if it responded to pure tones but only responded to narrow FM bandwidths (i.e. ≤5 kHz). An established technique was used to measure the 50% bandwidth of spectral and temporal tuning (see Sayegh et al., 2012, Morrison et al. 2014). For any given spike count function, the maximal count was used as a benchmark, with the lowest and highest stimulus values that evoked ≤%50 of the maximum count as the cutoffs for the spectral/temporal tuning bandwidths.

Temporally tuned FM cells had stereotyped response characteristics similar to the shortpass, bandpass, and longpass responses pure tone DTNs (see Aubie et al., 2009, Sayegh et al., 2011). The temporal tuning of FM cells can be described as either bandpass or fastpass. Bandpass cells respond to a specific range of sweep rates with spiking responses dropping to ≤50% of the peak response for FM rates both slower and faster than the best FM sweep rate (BR). Fastpass cells have a BR, but their spiking responses only drop to ≤50% of the maximum at slower FM sweep rates.

**2.3 Data analysis**

I used several measures to determine if temporally tuned FM cells in the IC were tuned to the stimulus duration or the rate of FM. First, a duration tuning function was generated using best CEF, best sweep bandwidth (SBW) pulses presented at +10 dB above threshold. Next, the sweep rate of the sound pulses was manipulated without changing the range of test durations. To do this, cells were stimulated with pulses that were varied in FM bandwidth (i.e. SBW x1, x0.5, and x2). The FM bandwidth of the pulses was set to half the SBW for one block and set to double the SBW for another after the initial block presented at the SBW was collected. With these three blocks of data, comparisons were made between BDs, sweep rates, and 50% temporal tuning bandwidths. If cells were tuned to pulse duration, the BD and excitatory temporal bandwidth should remain constant across absolute FM bandwidth changes. If cells are instead tuned to FM sweep rate, the BD and temporal bandwidth should increase linearly as the FM bandwidth increases (Figure 1).

*2.3.1 Bayesian comparison of rate and duration tuning*

Though my main research question was straightforward, it resists testing through traditional inferential methods. If cells are rate tuned, there should be no change across FM bandwidth conditions, a difficult thing to definitively say with a p-value without drastically transforming the data. Instead, I used a Bayesian model comparison method to determine which hypothesis (i.e. duration tuning or rate tuning) is supported by the data. This method examined the BD (dependent variable) measured across the three presented different sweep bandwidths (1x SBW, 0.5X SBW, 2x SBW; independent variable). A model was created for the two hypotheses assuming that each of the three BDs will fall on a line within some standard deviation (σ). The first model (H1) assumed that cells were tuned to FM duration so the line created by the set of three recorded BDs was flat (i.e. slope = 0), indicating no change in BD with changes in FM bandwidth. An alternative model (H2) assumed that cells were tuned to FM sweep rate, so the line created by the set of three recorded BDs was one with a non-zero slope that increases linearly with increasing FM bandwidth.

The analysis describes the likelihood, P, of obtaining the observed data, D, given the assumptions of each model. For example, in model H1, the likelihood of finding the observed data is given by P(D|Hi). The goal is to compute the Bayes Factor (BF), which is a proportional relationship describing the likelihood of the data given one model compared to the likelihood of the data given the alternative model, and is given by equation (1):

To compute the BF, the marginal likelihood of each model must be calculated. Each model was formulated as a hierarchical model, so that individual neurons, di, are analyzed based on how their temporal tuning responses match the expectations of each model and how those responses fit into the population of all cells, D. The marginal likelihood was calculated using the product rule so that the addition of each neuron’s data updated the likelihoods and prior expectations of each model as given by equation (2):

(1)

The marginal likelihood is equal to the likelihood of observing the first neuron’s data given the model, multiplied by the likelihood of the second neuron’s data given the first neuron’s data and the model, multiplied by the likelihood of observing the third neuron’s data given the second and the first neuron and the model, etc. To compute the marginal likelihood, the likelihood of observing each individual neuron’s data must be computed sequentially based on the assumptions of each model. Specifically, model H1 predicts that all of the neurons’ best FM durations, µi, are normally distributed around some population mean, M, and some standard deviation, S. Also, each individual neuron's measured BD values are normally distributed around the cell’s best FM duration, µ, with a known standard deviation, σ, based on measurement error (Figure 1). Similarly, alternative model H2 predicts that all of the neurons’ best FM sweep rates, ri, are normally distributed with some population mean, M, and standard deviation, S. Also, each neuron's measured BD values are normally distributed around the neuron's best sweep duration at the delivered stimulus bandwidth (BW), µ = BW/r, with a known standard deviation, σ (set to 2 ms in both models), based on measurement error (Figure 1). The range of values for M, S, µ, and r that is predetermined based on observations made during data collection (H1: M = 0.5-20, S = 0.1-2, μ = 0.5 – 20; H2: M = 0.5-20, S = 0.1-2, r = 0.125-5). In both models, the likelihood calculation for each individual neuron was as follows (the calculation for H2 was the same except that r was substituted for µ):

(3)

(2)

The likelihood of a data point was calculated given all the previous data points and the assumptions of the model. This likelihood was equal to the sum of the likelihoods of the neuron’s data given each value of µ multiplied by the likelihood of that value of µ given all the previous data points. The first term in equation (3) that must be calculated is the likelihood of the neuron’s data given a value of µ (or r) and that is given by these equations:

(4)

(5)

These are Gaussian functions for each of the three measured BD values (dk) against µ (or r). A visual representation is shown in Figure 1. If the neuron’s data was a close fit to a Gaussian function described by µ (or r) and σ, then that neuron strengthens the expectation for values consistent with the data and strengthens the likelihood for that model. All of the Gaussian functions for H1 are flat lines with a non-zero y-intercept and model the responses of a cell if it were duration tuned. Conversely, all of the Gaussian functions in H2 are linear functions with a y-intercept of zero and a slope of r, which model the responses of a cell as if it were rate tuned. When many neurons in the population are better described by Gaussian functions in H1 than in H2, then the marginal likelihood that H1 best describes the data will be higher than that of H2. Conversely, when many neurons in the population are better described by Gaussian functions in H2 than in H1, then the marginal likelihood that H2 best describes the data will be higher than that of H1.

Another term in equation (3) that must be calculated is the likelihood of a value of µ (or r) given all the previous data, which is computed by this equation:

Equation (6) is similar to the previous equations but instead of measuring data points against the mean for a cell, it measures the mean of a cell against the mean of the population given the posterior probability of the population mean and standard deviation (which are updated iteratively with each additional neuron). To evaluate equation (6), the posterior probability of M and S must be calculated. Starting with a uniform prior, the posterior probability is just a restatement of Bayes’ original equation (Bayes, 1763) and is given by this equation:

(7)

(6)

The posterior probability of any individual value of M and S is equal to the probability of the current data given M, S, and the model’s hypothesis multiplied by the prior probability of M and S given the hypothesis, all divided by the sum of those probabilities for every value of M and S. To calculate this, the likelihood of the current data given M and S must be calculated by:

(8)

The posterior probability of the data given M, S, and the hypothesis is equal to the sum, for all values of µ, of the likelihood of the data given a value of µ multiplied by the prior probability of that value of µ given M and S.

Finally, the marginal likelihood for each cell can be calculated using equation (3), which allows for the marginal likelihood for the whole dataset to be calculated using equation (2), which in turn allows both models to be compared and a Bayes Factor to be calculated in equation (1).

*2.3.2 Statistical analysis*

All data were measured from responses recorded at +10 dB re threshold. All statistical tests were calculated with IBM SPSS Statistics version 20. Independent samples t-tests were used to compare rate tuning response classes. Pearson’s r2 was used to measure the strength of correlation between variables.

**3. Results**

I recorded responses from 46 temporally selective neurons recorded from the IC of 25 big brown bats. All neurons had center frequencies within the spectral range of the fundamental acoustic element of the bat’s echolocation call (20-70 kHz). A majority of the cells were downward FM specialists (31/46) and responded very weakly or not at all when presented with upward FM sweeps. Some responded to both upward and downward FM sweeps (15/46), but I did not find any cells that responded exclusively to upward sweeps. One cell appeared to prefer upward sweeps based on a slighter higher average spike count. All were temporally selective for FM sweeps, but a small group were also selective for pure tones (13/46, 6 downward FM specialists, 7 non-specialists). Full temporal tuning data at each FM bandwidth for the Bayesian analysis was obtained from 35/46 cells, and the rest were included in other analyses to help describe the population as a whole.

**3.1 Organization and response properties of temporally tuned FM cells in the inferior colliculus**

A variety of tuning properties were correlated with a neuron’s center frequency. Tonotopic organization is a well-known property of mammalian auditory systems, wherein neurons are organized by their characteristic frequency along a gradient from low to high frequency. This finding has been repeatedly demonstrated for DTNs in the IC of bats (Casseday and Covey, 1992, Haplea et al., 1994, Grothe et al., 2001, Morrison et al., 2014), and my results from FM DTNs are no exception. The results support tonotopic organization with center frequencies of FM DTNs showing a strong positive correlation with electrode depth (Fig 2, r2 = 0.6572, p < 0.001). Visual inspection of the data shows that high proportion of neurons’ CEFs are clustered within the frequency range of 25-40 kHz. This pattern of CEF distribution may not be surprising as this spectral range corresponds to the fundamental harmonic of the echolocation calls generated by *E. fuscus* (Simmons et al., 1979, Casseday & Covey, 1992, Surlykke & Moss, 2000)*.*

Acoustic thresholds of FM responsive DTNs also showed some spectral organization. There was a positive correlation between CEF and threshold indicating that neurons with higher CEFs have higher thresholds (Fig 3A, r2 = 0.1271, p < 0.001). This relationship was more variable than tonotopy, with a wide band of thresholds seen across frequencies. This is particularly evident within the frequency range of 25-40 kHz, as Figure 3 shows that cells in this spectral range have thresholds ranging from 5-55 dB SPL. It is possible this is just a consequence of the middle ear filter function, as this distribution of thresholds corresponds with the behavioural audiogram of *E. fuscus* (Koay et al., 1995).

There were also organizational patterns involving the spectral and temporal characteristics of FM sweeps. The BR of neurons increased with center frequency (Fig 3B, r2 = 0.3191, p < 0.001), demonstrating that neurons that responded to higher frequencies also responded best at faster sweep rates. Best FM sweep bandwidths increased with increasing center frequency (Fig 3C, r2 = 0.2333, p = 0.001), indicating that cells tuned to higher frequencies responded best to wider FM bandwidths. Neurons that responded to high center frequencies were also less selective for frequency, independent of FM sweep bandwidth. The center frequency bandwidths (the range of center frequencies to which a cell will respond) also increased (Fig 3D, r2 = 0.0371, p = 0.035), meaning that neurons with high center frequencies respond to a wider range of sweeps, independent of how wide each individual sweep may be.

A majority of the recorded cells were bandpass filters for FM rate (34/46) with the rest being fastpass (12/46). Bandpass and fastpass FM rate cells differed in several important properties. Fastpass neurons had significantly higher CEFs than bandpass neurons (Fig 4, t = 4.510, p < 0.001) and were found at deeper electrode depths (Fig 4, t = 3.866, p < 0.001). Fastpass neurons also responded to a wider range of CEFs (t = 2.434, p = 0.019), had shorter best durations (t = 2.604, p = 0.013), and faster best sweep rates (Fig 4, t = 5.728, p < 0.001). Almost all fastpass cells also responded to pure tones (9/12), compared to a much lower proportion of bandpass cells (8/34). Almost all bandpass cells were downward FM specialists (27/34) compared to a much lower proportion of fastpass cells (4/12).

**3.2 Rate tuning versus duration tuning**

I observed both rate-tuned and duration-tuned FM cells in this study. Figure 5 shows examples of both types of cells and how their responses change as a function of stimulus duration. When evaluated as a function of stimulus duration, the spike counts from MU74.12 were similar across the tested bandwidths, all of which peaked at the same duration (2 ms, Fig 5A). On the other hand, its rate tuning profile changed across the tested FM bandwidths (Fig 5B). From these plots it appears that this cell is duration tuned. Conversely, the duration tuning profile of MU68.04 was quite variable. Its spike count functions changed quite dramatically across the tested FM bandwidths and peaked at different stimulus durations (Fig 5C). When its spike count was instead evaluated as a function of FM sweep rate (Fig 5D), it becomes clear that this cell is tuned to FM sweep rate. The spike count functions collapse onto each other and show the same pattern of excitation across FM bandwidths, even for off-BR FM sweep rates. A large majority of the recorded cells showed this visual pattern, but a quantitative method was needed to evaluate the temporal tuning properties of the population as a whole.

A Bayesian model comparison was used to determine how well neuronal responses match models of temporal tuning, either to FM rate tuning or FM duration tuning. For neurons that are rate tuned, BD should increase as the FM sweep bandwidth is increased, hence the rate tuning model expects a linear increase in BD with increasing FM bandwidth. If a neuron is FM duration tuned, then its BD should be unaffected by changes in sweep bandwidth assuming the FM bandwidth falls within the excitatory frequency response area of the cell. Examples of cells illustrating both types of responses are shown in Figure 6. For MU66.07, rate tuning is evident as the neuron’s best signal duration increases with increasing FM bandwidth in a roughly linear manner. The data points are better estimated by a linear function originating at zero than by a flat line with a non-zero intercept. This illustrates that the likelihood of finding those data points given the rate tuning hypothesis is much higher than given the duration tuning hypothesis. Conversely, for MU82.02, the best signal duration does not vary as a function of FM sweep bandwidth. The data points for this cell are better estimated by a flat line with an intercept of ~1.5 ms than by a line with a non-zero slope, so the likelihood of obtaining those data points given the duration tuning hypothesis is much higher than given the rate tuning hypothesis.

Figure 6 visually illustrates how the data points from individual cells are evaluated by each model. One cell is evidently duration tuned, so the data supports H1 more than H2, and vice versa for the other cell. To determine if the rest of the data supports rate tuning or duration tuning, these likelihoods are combined multiplicatively across the population. When more cells support rate tuning than duration tuning, then the marginal likelihood for H2 will be greater than the marginal likelihood for H1 and thus the calculated Bayes Factor (BF) should favor H2. Evaluating responses from the population, it is evident that in most cells, best duration increases with bandwidth (Fig 7). When the relative likelihoods were computed, the population data overwhelmingly supports a FM rate-tuning hypothesis (BF = 5.154 x 10155).

**4. Discussion**

**4.1 Cellular organization in the inferior colliculus**

Temporally selective FM cells showed similar trends to those seen in populations of pure tone DTNs in the IC. Unsurprisingly, FM cells exhibited tonotopic organization. Interestingly, more than 75% (36/46) of these cells had CEFs between 25-45 kHz, which is the same frequency range as the fundamental harmonic of the call made by *E. fuscus* when searching for prey (Simmons et al., 1979). This result is in line with previous reports of the IC of *E. fuscus*, where many pure tone DTNs are also clustered in this frequency range (Pinheiro et al., 1991, Haplea et al., 1994, Faure et al., 2003, Morrison et al., 2014). I observed several organizational patterns in the population of cells that would suggest that these FM cells play an important role in processing echolocation calls. Acoustic thresholds, sweep rates, and response bandwidths increased with increasing CEF. In the context of echolocation, FM cells with lower CFs would be tuned for the longer narrowband pulses emitted while searching for prey, while FM cells with higher CEFs would be tuned to respond to the short, loud, broadband pulses emitted by *E. fuscus* as it closes in on a prey item.

The organization of temporal response parameters in the population was also suggestive of a role in echolocation. It is evident from Figure 4 that temporal tuning in FM cells changes quite dramatically below depths of 1200 μm. The distribution of fastpass and bandpass cells suggests that the IC may have two functionally distinct sub groups of temporally tuned FM neurons. Fastpass cells very clearly had higher CEFs than bandpass cells. Fastpass cells also had faster sweep rates. Although the latter result may seem obvious, it is important to note that the term fastpass describes the FM filter characteristic of the cell, and is not directly related to the sweep rate that the cell prefers. For example, the FM filter function of a fastpass cell may peak at a lower sweep rate (i.e. ~3 kHz/ms) but it will still respond to a broader range of sweep rates than a bandpass cell that peaks at a higher sweep rate. Bandpass cells also had sharper center frequency bandwidths. Interestingly, almost all neurons with a preference for downward FM sweeps were bandpass cells (27/31) whereas FM neurons that were not directionally selective were almost evenly split between bandpass (7/15) and fastpass (8/15) categories.

These results suggest that the two sub groups may be specialized for different roles in the IC for the processing of auditory stimuli. Bandpass cells would function as specific filters for the identification of specific FM sweep rates, while fastpass cells would function as broader filters for detection of sounds that meet or exceed some minimum FM sweep rate. In terms of echolocation and foraging by *E. fuscus,* bandpass cells may be specialized for detecting the echoes of call emitted during the search phase which start at ~40-50 kHz and sweep downward to ~20 kHz over 10-20 ms (Surlykke & Moss, 2000). Search phase calls are emitted at relatively slower sweep rates (<2 kHz/ms) and it is evident in Figure 4 that bandpass cells are almost exclusively tuned to these sweep rates. Tuning for slow FM sweeps may be advantageous during the search phase because it would allow the bat to discern the echoes of its own calls reflecting off prey from the echoes and calls of other bats hunting nearby. Bats systematically increase the FM sweep rate of their calls during approach (Simmons et al. 1979, Surlykke & Moss, 2000) so calls emitted from nearby bats would likely have a slightly different FM sweep rate than the echoes the bat expects to hear from its own calls, and the sharply tuned bandpass cells may help the bat’s central auditory system to discriminate the subtle differences in these calls.

Fastpass cells appear to be specialized for the approach phase and the transition to the terminal phase of hunting. During approach, the increasing FM sweep rate means that the calls will become less and less similar to the calls being generated by nearby bats that are still searching for prey, so specific identification may become less important. Fastpass cells had broad spectral tuning with bandwidths than span the range of frequencies emitted during the latter end of the approach phase and beginning of the terminal phase (Surlykke & Moss, 2000). In this phase of hunting, the bat has already found a target and its goal is to hone in and capture the prey item. As the bat approaches, it detects echoes at a faster and faster FM sweep rate, so fastpass cells may function as an indicator that the bat is close enough to the target to initiate the feeding buzz (Simmons et al., 1979), at which point delay lines for detecting pulse-echo pairs would take over (Dear & Suga, 1995).

I did not find any other spatial organization patterns for temporal response parameters in the IC. This may have been due only measuring spatial differences along the vertical axis. A previous report from the IC suggests that FM cells may be organized along the anterior-posterior plane (Ehrlich et al., 1997), and if true then my spatial measurements were orthogonal to this cellular organization. Future studies using more precise spatial measurements in three dimensions could help elucidate this question.

**4.2 Mechanisms of temporal tuning in FM neurons**

This study was designed to determine the temporal tuning characteristics of FM cells in *E. fuscus.* I did not record the necessary data to make conclusions about the mechanisms creating rate tuning but it is worth discussing similarities between my results and previous reports to inform future studies on temporal tuning in FM neurons. There have been several mechanisms proposed to create temporal tuning in FM sweep neurons (for review, see Covey & Casseday, 1999). The ones potentially supported by my results include tuning for signal duration, asymmetric facilitation, and delayed high frequency inhibition. It is important to note that the mechanisms creating temporal selectivity for FM sweeps are by no means mutually exclusive as different mechanisms have been described within the same population of cells (Fuzessery et al., 2006).

When considering temporal tuning in FM-selective neurons, simple tuning for signal duration seems like a simple explanation, but current models for pure tone duration tuning do not include selectivity for FM sweep rate. A FM sweep lasting 4 ms can have a range of FM rates depending on the bandwidth of the sweep, and a cell strictly tuned to sweep duration could be excited by a wide range of sweep rates. Though I found a small number of cells whose responses were best described by duration tuning (i.e. true FM DTNs), rate tuning was by far more prevalent. Moreover, the “FM DTNs” may have been pure tone DTNs with extremely permissive frequency tuning as every one of these cells also responded to pure tones. Thus it seems unlikely that tuning for FM signal duration is a dominant neural mechanism.

Another type of temporal tuning for FM signals that has been proposed is created by delayed high frequency inhibition (Gordon & O’Neill, 1998, Brimijoin & O’Neill, 2005, Fuzessery et al., 2006, Fuzessery et al., 2011). In this model, the eRA of a FM neuron is flanked by a high frequency iRA that evokes inhibition after some delay. A fast sweep rate results in low frequency excitation and spiking before the onset of delayed inhibition evoked by higher frequencies. This model is similar to the anti-coincidence model describing shortpass duration tuning for pure tones, where shortpass cells will respond to sounds shorter than some maximum duration (Aubie et al., 2009). In the anti-coincidence model, an onset-evoked sustained inhibitory post-synaptic potential (IPSP) is evoked for the duration of the stimulus and an onset-evoked excitatory post-synaptic potential (EPSP) is evoked after some delay (i.e. the latency of the onset-evoked excitation is larger than the latency of the onset-evoked sustained inhibition). Thus, if a sound is short enough the IPSP will cease before the suprathreshold EPSP begins, causing spiking in the cell. When the tone duration is too long, the sustained IPSP will be overlap and be coincident with the EPSP, preventing suprathreshold excitation. Returning to the case of neurons responding to downward FM sweeps, a sustained IPSP would be evoked by a high frequency input and an EPSP would be evoked by a lower frequency input. This model was demonstrated by Fuzessery and colleagues (2006) who used two tones presented with some delay to map the eRAs and iRAs of these neurons, a method they termed “two tone inhibition”. They showed that this mechanism does not result in directional selectivity because upward FM sweeps starting in the cell’s eRA would evoke excitation before the sweep stimulates the iRA responsible for the delayed inhibition. Also, temporal tuning is abolished if the sweep does not start at a high enough frequency to evoke inhibition (Fuzessery et al., 2006).

Asymmetric facilitation can create directional selectivity by generating coincident offset-evoked excitation and inhibition for FM stimuli swept in one direction but not the other (Barlow & Levick, 1964, Sillito, 1977). This mechanism can also create rate tuning by using a combination of sub-threshold excitatory inputs with delays that create an input lag coherent with the excitatory sweep rate to create suprathreshold excitation (Fuzessery et al., 2006, Gittleman et al., 2009, Fuzessery et al., 2011). This mechanism was elegantly described by Williams & Fuzessery (2010) who demonstrated that two tones presented with a delay that was coherent with the excitatory FM sweep rate were sufficient to evoke spikes from temporally tuned FM neurons, a paradigm they termed, two-tone facilitation. For example, a hypothetical neuron could have two excitatory inputs, one evoked by 50 kHz sounds with a delay of 2 ms and the other evoked by 45 kHz sounds with a delay of 1 ms. Because the input lag is 1 ms and the input frequencies are 5 kHz apart, when the sweep rate is 5 kHz/ms, the two excitatory inputs will be coincident and evoke suprathreshold excitation. This cell will respond to a FM sweep from 55🡪40 kHz with a 3 ms duration, but if the sweep rate were slower (i.e. a sweep from 55🡪40 kHz with a 6 ms duration), or in the other direction (i.e. from 40🡪55 kHz with a 3 ms duration), the inputs would not be coincident and thus would not cause suprathreshold excitation. In this way, neurons are tuned to FM sweep direction and rate but not duration. Changing the bandwidth alters the time between the evoked excitatory inputs, which changes the best excitatory duration: a wider bandwidth will evoke responses at longer durations and a narrower bandwidth will evoke responses at shorter durations.

My results reveal that there are at least two distinct classes of FM neurons: fastpass and bandpass. Rate tuning in these classes appears to be created through separate mechanisms. Rate tuning in bandpass FM neurons appears to be created through asymmetric facilitation, as the response properties of these cells line up closely with those reported by Williams & Fuzessery (2010). Less than 25% (8/34) of the bandpass neurons responded to pure tones, and a large majority (27/34) were downward FM specialists. Furthermore, many had relatively narrow best sweeps bandwidths (~2 - 8 kHz), and responded to a range of center frequencies that was wider than the best sweep bandwidth. This means that in most cells, the presence of high frequency inhibition was not required to create rate tuning as excitatory sweeps could be entirely contained within the excitatory frequency response area (i.e. MU79.02 responded to sweeps with CEFs ranging from 29-36 kHz, but its SBW was only 2 kHz). I did not test this hypothesis through a two-tone facilitation paradigm (described above; see Williams & Fuzessery 2010), but it would be interesting to see if such a paradigm could be used to describe temporally tuned FM cells in *E. fuscus*.

The group of fastpass cells I found are likely temporally tuned through high frequency inhibition. These neurons typically had very wide sweep bandwidths, almost all of them responded to pure tones (10/12), and only a third (4/12) were directionally selective for downward FM. And, the 2 neurons that did not respond to pure tones were both directionally selective for downward FM and were found at depths ≤1200 μm, meaning that they could have potentially been bandpass cells. Unfortunately, I did not stimulate them with fast enough sweep rates to definitively reach this conclusion. Both a response to pure tones and a lack of directional selectivity are indicative of rate tuning through delayed high frequency inhibition (Fuzessery et al., 2006, 2011), suggesting that this group of fastpass cells were tuned in this manner. This hypothesis could be further tested with a two-tone inhibition paradigm to map the eRAs and iRAs and to determine the time course of inhibition in these cells.

**4.3 Temporal tuning for rate and duration**

This study was inspired by an earlier study in the IC of *E. fuscus* that reported that some DTNs were tuned to the duration of FM sweeps (Ehrlich et al., 1997). I sought to answer whether these so-called “FM DTNs” were tuned to stimulus duration in the same manner as the well documented pure tone DTNs or if the cells were FM rate-tuned and thus should be considered as an entirely different class of temporally tuned neurons. I developed a hierarchical Bayesian model to measure whether data from an individual cell was better represented by a model assuming duration tuning of FM rate tuning. By combining the relative measurements from every cell into a hierarchical model, I computed whether responses from the population of FM cells were better described by rate tuning or duration tuning. The analysis revealed that some FM cells were perhaps tuned to stimulus duration; however, across the population as a whole, most temporally-selective FM cells were better represented by a model of rate tuning than by a model of duration tuning. Furthermore, every one of the cells that was found to be duration tuned also responded to pure tones, so there is the possibility that these cells were just classic pure tone DTNs with extremely wide frequency selectivity and thus were not filtered out by my exclusion criteria. Therefore, I conclude that previous studies reporting the existence of FM DTNs were likely reporting from cells that were tuned to the rate of FM.

That FM neurons were better described as rate tuned than duration tuned was not surprising as rate-tuned FM neurons have been reported in both the mammalian IC (Poon et al., 1991, Ehrlich et al., 1997) and auditory cortex (Heil et al., 1992, Mendelson et al., 1993, Ricketts et al., 1998). In particular, rate tuning has been extensively studied in auditory pathway of the pallid bat (Fuzessery, 1994), a species with similar echolocation behaviour to *E. fuscus*. My study reports a population of FM neurons similar to that found in *A. pallidus*, but in *E. fuscus* there appears to be an emphasis on cells tuned to downward FM. A majority of cells recorded in my study responded exclusively to downward FM sweeps (~67%) while only 13% of those reported by Fuzessery (1994) were downward FM-specialists. Furthermore, only 28% (13/46) of the cells recorded were also duration tuned for pure tones, compared to 50-60% of FM cells showing this selectivity in *A. pallidus*. This difference may reflect differences in the echolocation behaviour between the two species. Big brown bats rely on echolocation for both orientation and prey detection, as they consume small flying insects (Simmons et al., 1979, Masters et al., 1985). In contrast, pallid bats use echolocation for orientation and hunting but they can also use passive hearing to detect and localize faint prey-generated sounds of orthopteran and coleopteran insects (Fuzessery et al., 1993, Lenhart et al., 2010). Higher central auditory centres of *A. pallidus* appear to separate auditory processing into two distinct streams to analyze both types of sounds (i.e. FM sweeps and broadband noise bursts, Razak & Fuzessery, 2007) and this may explain why the auditory midbrain of *A. pallidus* shows less specialization for downward FM sweeps compared to *E. fuscus*.

**4.4 Conclusion**

The main goal of this study was to determine if temporally tuned FM cells in the IC of *E. fuscus* were duration-tuned as previously reported or if they were a separate class of temporally tuned neurons (i.e. rate-tuned neurons). The results show that an overwhelming majority of these FM DTNs are better described as rate tuned, suggesting that FM sweep rate is the dominant temporal parameter for temporal selectivity of FM sweeps in the IC. Future studies on these neurons should use two tone stimuli to better elucidate the neural mechanisms creating rate tuning in *E. fuscus* and use precise spatial measurements in three dimensions to better map the organization of temporally tuned FM cells in the IC.

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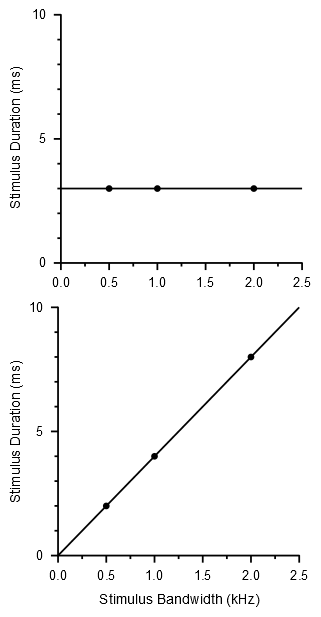
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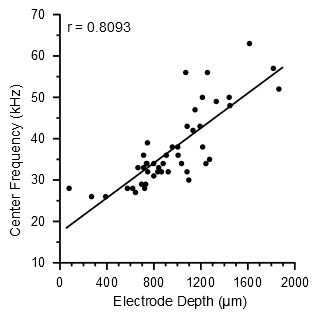
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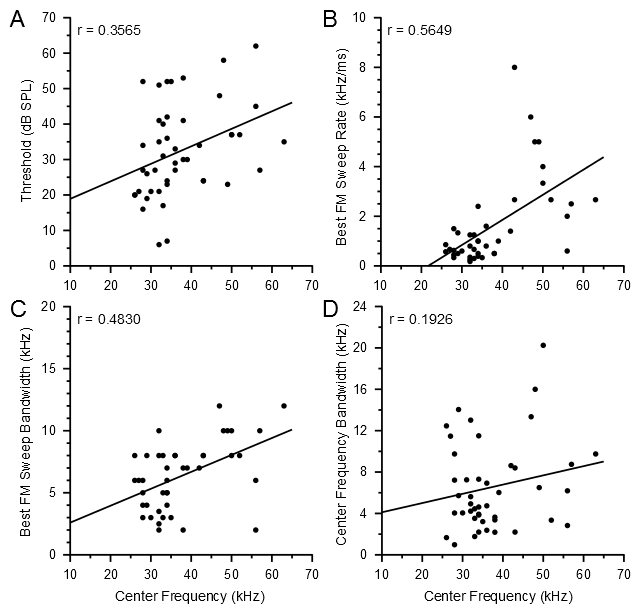
**6. Figures**



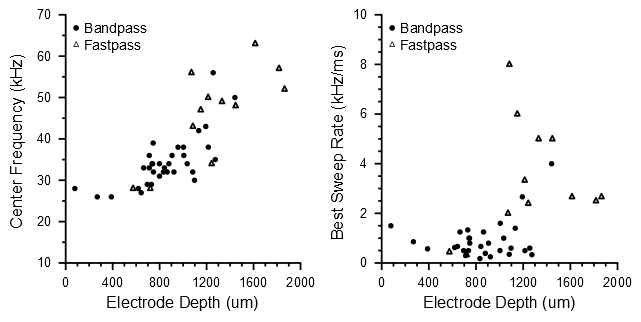
**Figure 1: Visual representation of theoretical hypotheses H1 and H2**. In H1 (upper panel), the cell is assumed to be duration tuned so each of the measured best duration remains constant when measured at different spectral bandwidths. The cell’s best durations should all fall on the solid line with an intercept representing best duration, µ, within some standard deviation, σ (dashed lines), which represents the measurement error. In H2 (lower panel), the cell is assumed to be rate tuned so its best duration should increase linearly with sweep bandwidth. The best durations should fall on the solid line with a slope, r, (which represents the predicted change in best duration across bandwidth such that μ = BW/r) within some standard deviation, σ (dashed lines).

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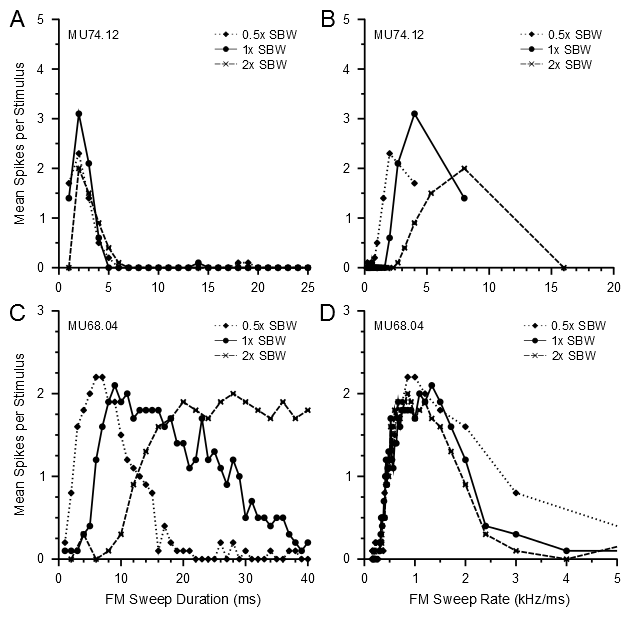
**Figure 2: Tonotopy in FM neurons.** Temporally tuned FM cells are tonotopically organized in the IC of *E. fuscus.* Note the dense cluster of neurons in the range from 600-1200 μm that have CEFs between 25-40 kHz. This bandwidth corresponds to the fundamental harmonic of the bat’s echolocation pulse.



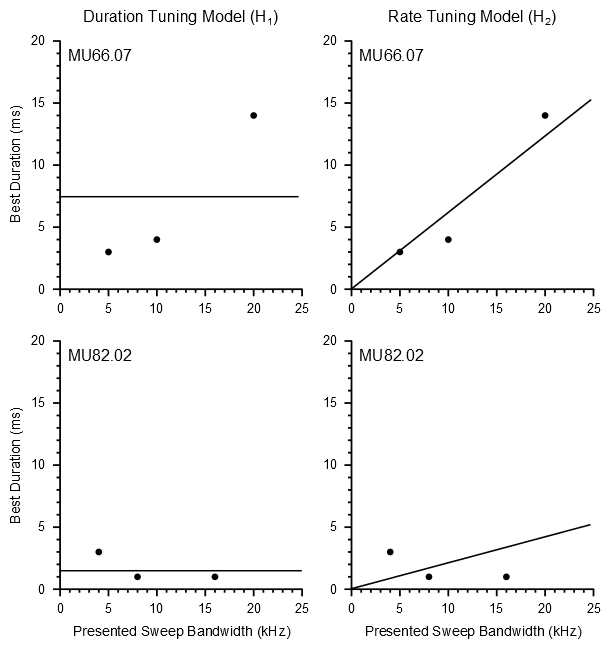
**Figure 3: Organization of response characteristics of temporally tuned FM cells in the IC.** *(A)* There was a weak positive correlation between acoustic threshold and CEF. Within the CEF range of 25-40 kHz the IC appears to have a wide range of neuronal acoustic thresholds. *(B)* There was a strong positive correlation between best sweep rate and CF. At higher frequencies, the range of sweep rates to which neurons are tuned is much wider. *(C)* There was a moderate positive correlation between best FM sweep bandwidth and CF. *(D)* There was a weak positive correlation between center frequency bandwidth and CF, suggesting that not only did neurons responding to higher frequencies prefer wider sweep bandwidths as shown in (C), these neurons also responded to a wider spectral range of sweeps.

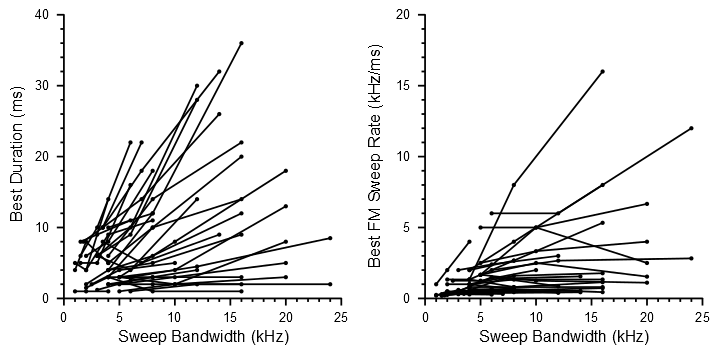
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**Figure 4: Response classes of temporally tuned FM cells.** *Left panel.* Fastpass cells had significantly higher CFs and were found at significantly deeper electrode depths in the IC. *Right panel.* Fastpass cells also had significantly faster sweep rates. From these plots it is evident that there is a shift from bandpass tuning to fastpass tuning below ~1200 μm in the IC.

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**Figure 5: Spike count functions for two temporally tuned FM cells.** Each plot shows the mean spikes per stimulus at +10 dB above threshold in response to FM pulses that were randomly varied in duration and presented in three blocks, each at a different FM bandwidth (i.e. 0.5x SBW, 1x SBW, 2x SBW). In the left column, spikes are plotted as a function of stimulus duration. In the right column, spikes are plotted as a function of the FM sweep rate of the stimulus (FM sweep rate = SBW/stimulus duration). The spike count functions for MU74.12 suggest that the cell is duration tuned, as its spike count as function of stimulus duration is tolerant to changes in FM bandwidth, but its spike count as a function of FM sweep rate does not show the same tolerance. Alternatively, the spike count functions for MU68.04 indicate that the cell is rate tuned. Its spike count as a function of stimulus duration changes when the FM bandwidth is changed, but its spike count as a function of sweep rate is tolerant to changes in FM bandwidth. A majority of the cells recorded show this pattern of rate tuning (30/35; see figure 6).

**Figure 6: Examples of Bayesian estimation in both theoretical models.** This figure illustrates how the data recorded from DTNs are expected to fit into each theoretical model by plotting the measured best durations (i.e. maximum spiking response) from two DTNs (MU66.07 and MU82.02) and the best estimations from each theoretical model. Each cell was stimulated at three FM bandwidths, the best sweep bandwidth (SBW), half of SBW, and double SBW. The duration tuning model predicts no change in best duration with FM bandwidths, so the data should fit a horizontal line. The rate tuning model assumes a linear increase in best duration, so a line with some slope and a y-intercept of zero was fit to the data. The top row depicts how data recorded from MU66.07 fits into each model and the bottom row depicts how data recorded from MU82.02 fits into each model. The data recorded from MU66.7 suggests the cell is rate tuned for FM stimuli as even the best horizontal line is a poor fit. The marginal likelihood computed by the duration tuning model is much lower than the marginal likelihood generated by the rate tuning model (P(Di | H1) = 1.6 x 10-6, P(Di | H2) = 6.4 x 10-3). The data recorded from MU82.02 suggests the cell is duration tuned for FM stimuli a horizontal line (i.e. slope = 0) fits the data better than a sloped line starting at the origin. The marginal likelihood computed by the duration tuning model was greater than the marginal likelihood computed by the rate tuning model (P(Di | H1) = 1.7 x 10-3, P(Di | H2) = 1.7 x 10-4).



**Figure 7: The effect of FM bandwidth on duration tuning and FM rate tuning in the IC.** In the left panel, the measured best duration (i.e. the stimulus duration that evoked the maximal spiking response) at each stimulus FM bandwidth is plotted for every cell. In almost every cell (30/35), the best duration increases with increasing sweep bandwidth. In the right panel, the measured best sweep rate (i.e. the FM sweep rate that evoked the maximal spiking response) at each FM bandwidth is plotted for every cell. For most cells (30/35), the sweep rate remains constant with increasing bandwidth. For this figure, cells were scored based on how their data supported each model hypothesis (i.e. if the recorded data supported H2 more than H1, the measured best duration increased with increasing FM bandwidth).