

ABSTRACT

Title of Thesis: LOCAL FIELD POTENTIAL ANALYSIS OF
BEHAVIORAL TASK INDUCED
PLASTICITY IN HIGHER-ORDER
AUDITORY CORTEX

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Previous studies have shown attention related transient changes induced during auditory discrimination behavioral tasks in primary auditory cortex (A1). This study involved awake, behaving ferrets performing similar auditory tasks with negative reinforcement; however, recordings were focused on higher-order cortical areas to understand what, if any, plastic effects exist and how they compare with A1.

Although neurons in the posterior ectosylvian gyrus (PEG) exhibit similar tuning properties and conform to a tonotopic mapping consistent with prior findings, these areas enhance selectivity to target stimuli. The neurophysiological recordings from A1, PEG, and frontal cortex were then compared using the local field potential (LFP). This analysis focused on the response-power changes within these recordings and findings were consistent with single unit trends.

LOCAL FIELD POTENTIAL ANALYSIS OF BEHAVIORAL TASK INDUCED
PLASTICITY IN HIGHER-ORDER AUDITORY CORTEX

by

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Dedication

Hold fast to dreams
For if dreams die
Life is a broken-winged bird
That cannot fly.

Hold fast to dreams
For when dreams go
Life is a barren field
Frozen with snow.

- Langston Hughes

This work is dedicated to my loving wife and family for their unwavering support and encouraging me to hold fast.

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Chapter 1: Introduction

The auditory cortex has been a focus of study in understanding the perception and localization of complex sound stimuli. Many neurophysiological experiments have helped reveal more about the auditory processing performed by this cortical area. While there is still much to explore, one effect that has been shown to exist in the auditory cortex is plasticity, the change in strength of synapses over time (Hughes, 1958).

Plasticity is a crucial aspect of nerve cell behavior with regards to memory and higher brain functions (Eric Kandel, James Schwartz, 2014). These changes in synaptic strength can take place over longer periods of time, on the order of days, weeks, or months and can be as dramatic as remapping a cortical area. This form of plasticity may occur after some trauma to a particular area of the brain. In order for the brain to revive some ability to process environmental stimuli, the cortical map can be reshaped onto a portion of the unaffected brain (Sur, Garraghty, & Roe, 1988). Additionally, long-term plasticity can be examined by comparing the cortical characteristics of animals trained on a particular skill or task with untrained animals. These trained animals can have differences in cortical temporal and spectral characteristics, receptive fields, and response latency when presented with the stimulus they have been conditioned to (Edeline and Weinberger, 1993, Recanzone et al., 1993; Elbert et al., 1995). Many of the recordings from the long-term plasticity studies were done with animals under anesthesia and not actively engaged in the task they had been trained on.

Evidence of plasticity has also been shown to occur more rapidly during the behavior of a stimulus-based task. The effects may be less drastic than those described previously but they may include changes in the firing rate or temporal precision of the neurons of a particular cortical area. The synaptic changes that occur during behavior may persist for a short duration following the task but eventually return to non-behavioral baselines. Although more subtle than a full cortical remap, this finding is important for understanding the effects of a behavioral task on the animal's brain. Additionally, this illuminates that when sound takes on a particular meaning, the auditory cortex shows changes that affect the animal's sensitivity to the stimulus and thus has an effect on the perception. Ultimately, this rapid plasticity may be an important aid in the animal performing the behavioral task correctly based on the stimulus.

Our laboratory has an experimental model for eliciting rapid plasticity evidenced by neurophysiological recordings from the auditory and frontal cortex of awake, behaving ferrets. This model is used to collect data giving us some insight into the neural processing taking place and how sounds that have a behavioral meaning influence rapid changes in processing being done by the brain.

Chapter 2: The Auditory System

The auditory system encompasses everything from the outer ear, where sound stimuli are first captured and funneled into the ear, through the various connections until the sensory information is processed by the auditory cortex. The following sections provide an overview of the role of each portion along the path from signal capture to perception.

2.1 Transduction

The outer ear directs sound into the ear canal leading to the tympanic membrane. Mechanical energy of sound waves vibrating this membrane is transferred, by the three ossicles of the middle ear, to produce movement of the cochlear fluid via the oval window.

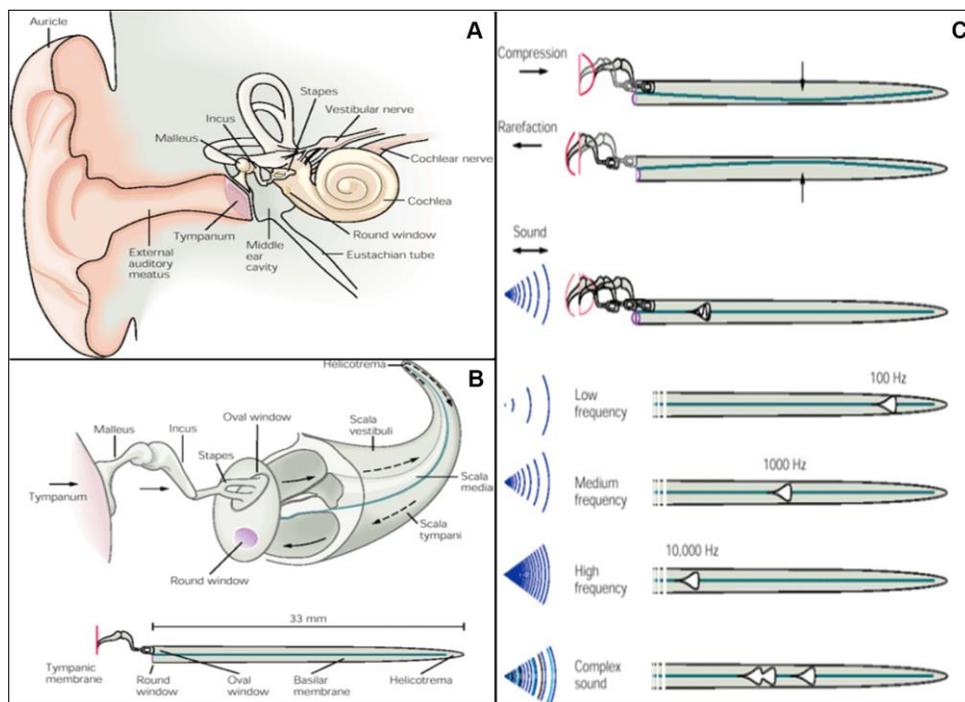


Figure 2.1: Overview of sound transduction (A) Schematic of the human ear (B) The cochlea pictured as if it were uncoiled (C) Sound transduction along the basilar membrane (Kandel et al 2000)

The effect is a vibration of the basilar membrane in the cochlea. It is the variation in mechanical properties along the basilar membrane, thicker and more taut at the base gradually moving to a thin and floppy apex, that gives rise to the first step in frequency analysis (Kandel et al 2000).

The cilia of the organ of Corti are responsible for the mechano-electrical transduction in the cochlea. The inner hair cells along the basilar membrane have characteristic frequencies, the frequency at which the cell is most excitable, which vary smoothly and monotonically in a logarithmic manner. This tonotopy is a reoccurring theme of the auditory system as information passes through the pathway to the auditory cortex. Nerve fibers innervate the inner hair cells to transmit stimulus frequency and intensity information to the cochlear nucleus via cranial nerve number VIII.

2.2 Central Auditory Pathway

The cochlear nucleus is the first stage of auditory stimulus processing. It preserves high fidelity temporal and spectral information as it passes the neural encoded sound stimulus along parallel pathways. Three main parallel pathways starting from the anteroventral, posteroventral, and dorsal cochlear nuclei project acoustical information along to the superior olivary complex (SOC). Each pathway contributes to the analysis of different sound attributes such as localization due to interaural time delays or intensity differences.

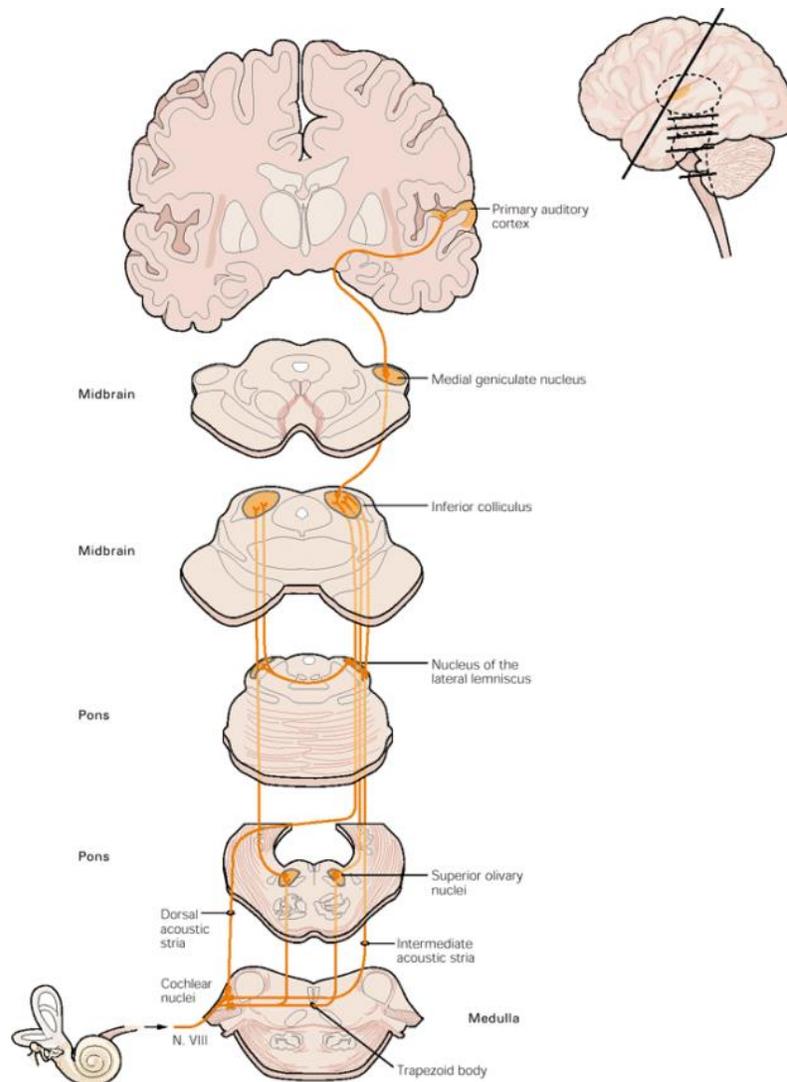


Figure 2.2: Central auditory pathway from cochlear nucleus to auditory cortex (Kandel et al. 2000)

The Inferior Colliculus (IC) appears to be the first point of convergence for acoustic information stemming from sound stimulus effects being projected along the auditory pathways. The IC integrates this information from multiple paths to form a coherent auditory scene. The Medial Geniculate Body (MGB) is the next step along the pathway to the auditory cortex of the brain and this commences the analysis of the auditory scene. In effect, the MGB begins the process of sound perception (Eggermont, 2001).

2.3 Auditory Cortex

The ascending auditory pathway prominently projects onto the primary auditory cortex, a dorsal surface portion of the temporal lobe. The auditory cortex carries the theme previously discussed of a tonotopic mapping. A gradient exists of low to high characteristic frequencies of neurons from the rostral to caudal section of primary auditory cortex, respectively. A one-dimensional spectral investigation will yield this receptive field, the description of optimal inputs eliciting the strongest responses from neurons.

In order to capture additional receptive field properties of the auditory cortex, a two-dimensional analysis can be done. Looking at the neural responses from spectral and temporal input modulation, a time-dependent spectral transfer function may be obtained. This spectro-temporal receptive field (STRF) is a linear mapping from the sound spectrogram to the neural response (Klein, Depireux, Simon, & Shamma, 2000). In the studies discussed later in this paper, the stimuli are thirty instances of temporally orthogonal ripple combinations (TORCs). The STRFs can be measured by reverse correlating with the spectra of the TORC stimulus. The STRF is limited as it is a linear model of a non-linear system. However, it is a powerful tool for better understanding cortical processing, particularly in primary auditory cortex where temporally quick and phase locked responses exist.

Chapter 3: Higher-Order Auditory Cortex Plasticity

3.1 Introduction

The auditory cortex is a major site of auditory scene perception. One important investigation is the effects on auditory processing undergone during a sound stimulus dependent behavioral task. A number of studies have demonstrated rapid, short-term task-dependent changes in the primary auditory cortex (A1) (J. Fritz, Elhilali, & Shamma, 2003) as well as in the dorsolateral frontal cortex (dlFC) (J. B. Fritz, David, Radtke-Schuller, Yin, & Shamma, 2010) of ferrets. In this study, we looked into the higher areas of the auditory cortex, specifically the posterior pseudosylvian field (PPF) and the posterior suprasylvian field (PSF). These two areas are adjacent to A1 and when grouped together, are referred to as the dorsal posterior ectosylvian gyrus (dPEG).

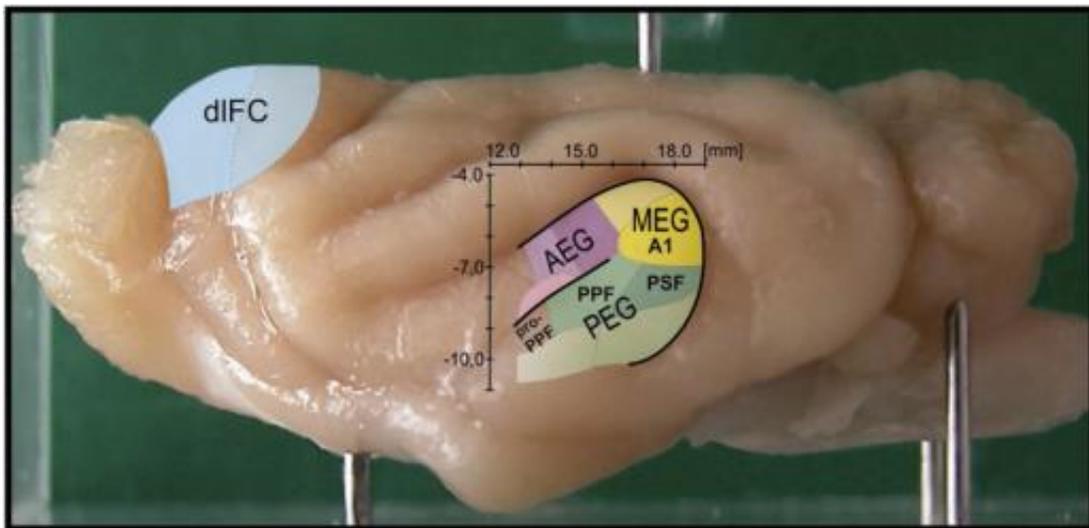


Figure 3.1: Lateral view of ferret brain with auditory and frontal cortex overlay (Atiani et al., 2014)

Various attention-related effects have been illuminated by previous studies of A1. Neurons in A1 undergo rapid, reversible changes in sensory tuning properties in such a way as to enhance the contrast between stimuli relevant to the task and those of the auditory background. The studies involving dlFC show a more abstract representation of the stimuli that reflect the behavioral meaning of the sound. This is presumably influential in behavioral decisions and may possibly contribute to top-down signals that foster task-related changes in receptive field properties. The intent of this study is to examine these two higher order cortical areas, PPF and PSF, to potentially elucidate their function in the sensory perception. Analysis of neurophysiological recordings from dPEG would potentially show a blending of the effects seen in A1 and dlFC. However, it is expected that the overall effect would remain in accordance with these two previously studied areas and contribute to the enhancement of the target stimuli the animal uses to make a behavioral decision.

3.2 Methods

3.2.1 Stimuli

The behavioral task was presented in blocks of trials consisting of reference sounds and pure tone targets. The reference sounds utilized were either temporally orthogonal ripple combinations (TORCs) or narrowband noise (NBN). TORCs were chosen at random from a set of 30 different TORCs which each span 5 octaves. The target used in this study was a pure tone of length 1.0 or 1.5 seconds and varied frequencies. Although within a given block of behavioral trials, the target frequency was consistent. The duration and level (between 60 and 75 dB) of reference and target sounds was the same in a single experiment.

3.2.2 Behavioral Task Training

Adult female ferrets were trained on a pure tone detection task using conditioned avoidance. The trials consisted of reference stimuli (between one and six TORCs) followed by a pure tone. The only exception to this trial block construction is a catch trial with a seventh TORC and no pure tone target. Water flows continuously from a spout in front of the animal and the ferret can lick freely during reference sounds until they hear a pure tone. If the ferret licks the waterspout following the tone, this is considered a miss and the animal receives a mild shock. If the animal successfully refrains from licking during the post stimulus window, the trial is considered a hit. Animals were trained on this pure tone detection task until they achieved at least an eighty percent hit rate consistently while maintaining less than a twenty percent false alarm rate.

3.2.3 Surgical Implant

Once consistent behavioral performance was achieved, the animals underwent a surgical procedure to mount a stainless steel headpost to the skull. Anesthesia was induced using Ketamin-Xylazine and the ferrets were kept anesthetized with isoflurane (1%-2%) throughout the remainder of the procedure. The steel post was attached to the skull of the ferret using a combination of stainless steel screws and bone cement. Access ports were left in the bone cement providing access to the skull covering the auditory cortex as well as frontal cortex. The ferrets were given antibiotics and analgesics following surgery as necessary.

Recovery time for the headpost implantation procedure was approximately two weeks. Following recovery, the ferrets were habituated over a period of one to two weeks, to the apparatus used during recordings. The animal rig consisted of a Lucite horizontal cylindrical holder to prevent large body movements as well as a head restraint attached to the headpost previously implanted. This restraint system was key in producing stable recordings throughout subsequent neurophysiological experiments. The ferrets, while restrained in the holder, were retrained on the behavioral task previously described for two to three weeks prior to commencing neurophysiology.

3.2.4 Neurophysiology

Small craniotomies, 1-2 mm in diameter, were made over the auditory cortex prior to recording sessions. Each neurophysiological recording session lasted between six and eight hours and were conducted in a double-walled, sound-attenuating room. Recordings were captured via high impedance (2-6 M Ω) tungsten electrodes (between one and four electrodes per recording) and the Alpha-Omega recording system. The recording apparatus maintained approximately 500 μ m between each of the electrode's closest neighbors and provided independent movement of each electrode in the holder. The electrodes were advanced until good isolation was found, prior to starting the behavioral tasks and recording. A software suite written in MATLAB is used after the experiment to isolate single units from the multiunit spike waveforms.

A combination of multiple methods was used to find the primary auditory cortex (A1) and subsequently the higher order cortical areas of interest for this study. The approximate location of A1 can be reached by measuring 12 mm anterior to the back ridge of the ferret's skull and 8 mm from the middle ridge of the skull. A craniotomy is made in this location and initial recordings are done to get general properties of the neural response. The neurons in A1 have a short latency (14-24 ms) in addition to phase locking to the onset of tones. Lastly, a tonotopic gradient exists along the dorsoventral axis of the brain such that best frequency responses of neurons move from high to low frequencies as recordings are gathered from dorsal to ventral areas, respectively. These three contextual clues allow us to positively identify A1 and subsequently move recording sites more ventrally until the tonotopy reverses. As the tonotopy reverses, response properties also change such as longer latencies and longer sustained responses. These changes are indicative that the recording is in the dorsal posterior ectosylvian gyrus (dPEG) (Bizley, Nodal, Nelken, & King, 2005). Within dPEG, the sub-areas are identified using a tonotopic gradient along the rostrocaudal axis with a tonotopic reversal in low frequencies at the boundary between PPF and PSF (roughly perpendicular to the A1 boundary).

3.3 Results

3.3.1 Passive Auditory Tuning Properties

Recordings were conducted while awake animals passively listened to broadband noise and pure tones to collect data for comparing basic tuning properties of A1 and higher-order auditory cortical areas. The two sub-areas of dPEG, PPF and PSF, exhibit very similar neural response properties and for this analysis can be grouped

together when comparing them to primary auditory cortex. A1 and dPEG exhibit similar distribution of frequency tuning with a slightly broader tuning bandwidth on average in dPEG. A more significant difference between these two areas of auditory cortex exists in their temporal dynamics. In general, A1 neurons are quicker than those found in dPEG and have a propensity to have shorter onset latencies. Exacerbating this temporal difference is longer response duration of dPEG neurons on average.

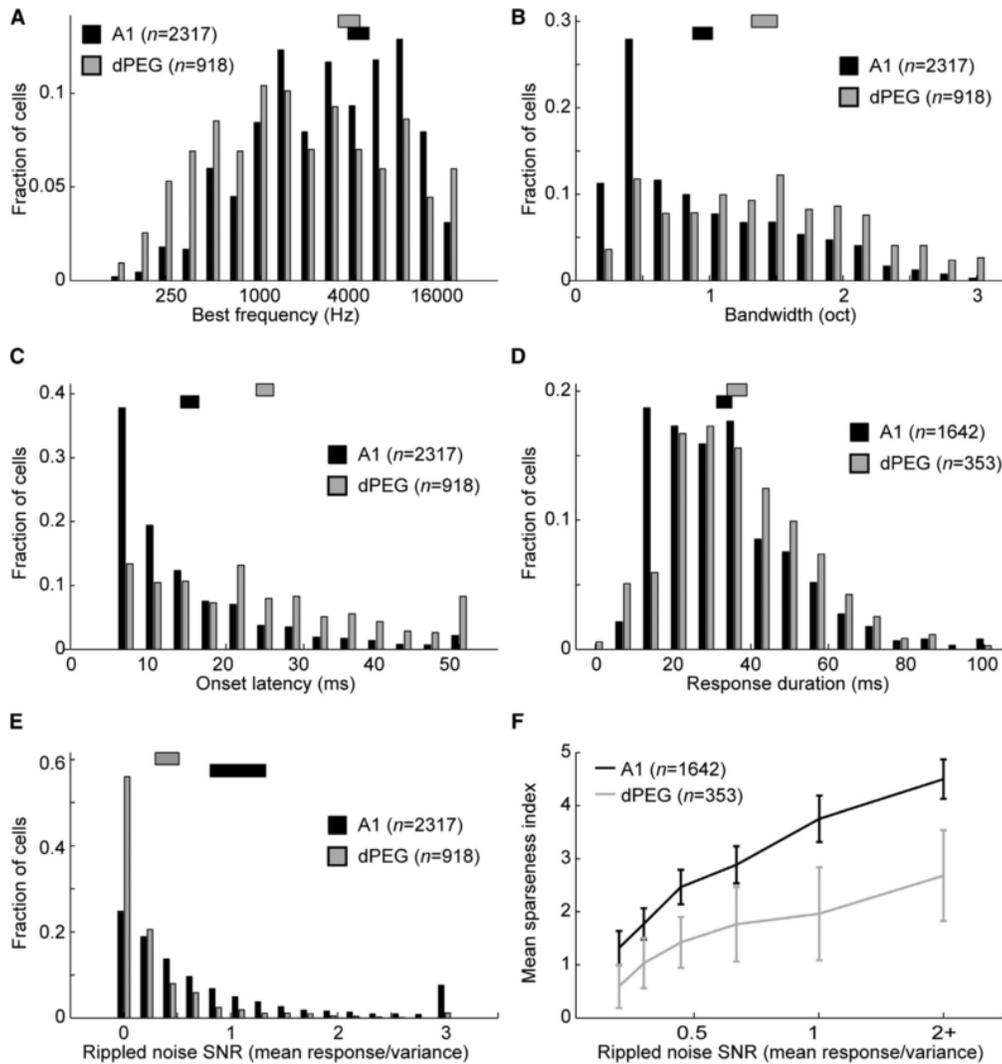


Figure 3.2: Auditory tuning comparison of A1 and PEG (A) best frequency (B) frequency tuning bandwidth (C) onset latency (D) response duration (E) signal-to-noise ratio (F) STRF sparseness index (Atiani et al., 2014)

The recordings from dPEG were less likely to identify neurons that reliably displayed phase-locked responses to TORCs. Phase-locking was measured by the signal-to-noise ratio (SNR) of the time-varying response to these broadband rippled noise stimuli (Atiani et al., 2014). The result of this weaker phase-locking in dPEG is the necessity to measure the influence of the behavioral task via changes in amplitude and peristimulus time histogram (PSTH) response dynamics as opposed to changes in the STRFs as done in previous auditory cortex studies. A similar comparison of reference to target responses was done in a previous study for the frontal cortex where there is virtually no phase-locking (J. B. Fritz et al., 2010).

3.3.2 Target Enhancement in Secondary Auditory Cortex

The animals' neurological activity in auditory cortex (A1 and dPEG) was recorded while they performed the auditory discrimination task described previously. Additionally, recordings were conducted while the animals passively listened to the auditory stimuli pre- and post-behavior. Comparing the passive and behaving conditions PSTH responses to task stimuli assessed the plastic effects of the behavioral task.

The auditory task illuminated three distinct, statistically significant patterns of PSTH response effects in roughly 42% of cells recorded from dPEG (Atiani et al., 2014). The figure below shows an example of each type of change observed in the PSTH responses between passive and active auditory stimulus presentation. One effect is a sustained enhancement to the target tone during behavior combined with a slight suppression to the reference stimulus. The second effect is a substantial decrease in

responses to the reference sound during the behavioral task. The final effect observed was a significant increase in response to the target tone and only a mild suppression of the reference while actively listening. Overall, these three distinct patterns of PSTH changes during behavior produce an enhancement of the target tone during behavior and the PSTH generally returns to the pre-passive baseline after the behavioral task was completed.

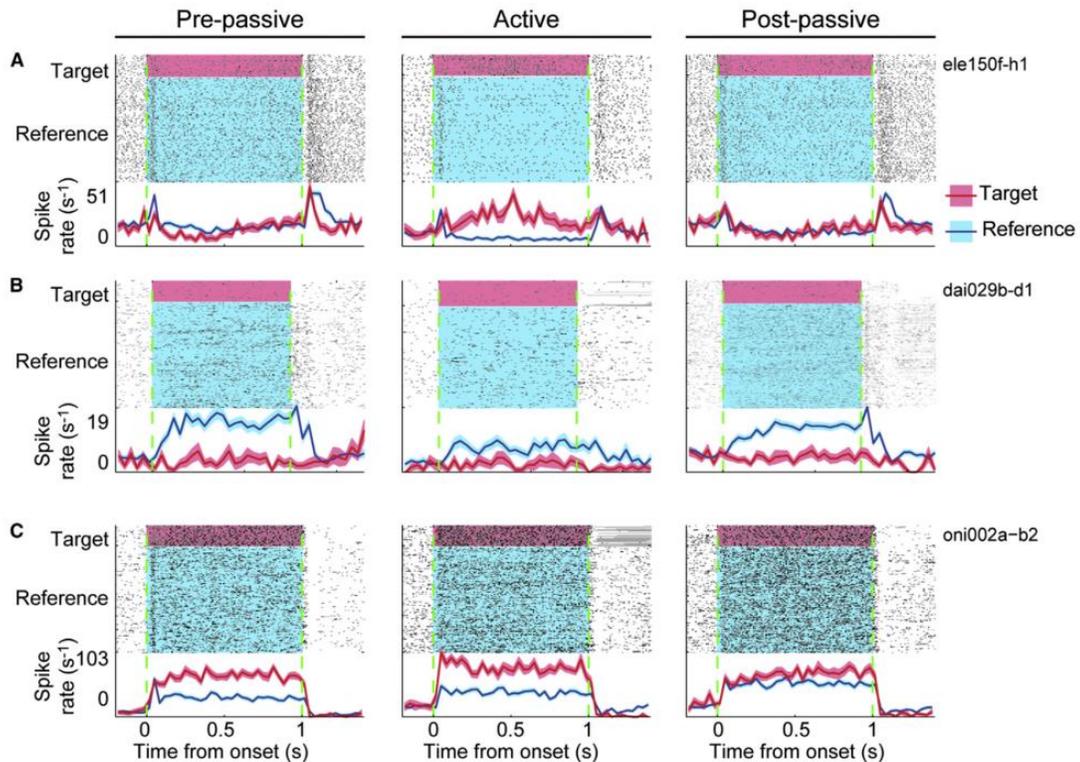


Figure 3.3: The response of three PEG neurons to target and reference stimuli before, during and following behavior depicted with raster plots show the general trend of increasing discrimination between reference and target stimuli (A) Overall increase and sustained response to target stimulus during behavior with a slight suppression to reference (B) Significant decreased reference response during behavior (C) Increased spiking rate for targets during behavior (Atiani et al., 2014)

3.3.3 Target Enhancement throughout the Auditory Processing Hierarchy

The PSTH responses were normalized for each neuron's response with respect to its maximum magnitude and sign. The population PSTH response for each cortical area (A1, dPEG, and dlFC) was obtained by averaging the normalized PSTHs for all

neurons within a given area that, during behavior, showed a significant change in their response to the sound stimuli. The auditory behavioral task induced progressively larger changes moving upwards in the auditory processing hierarchy (Atiani et al., 2014).

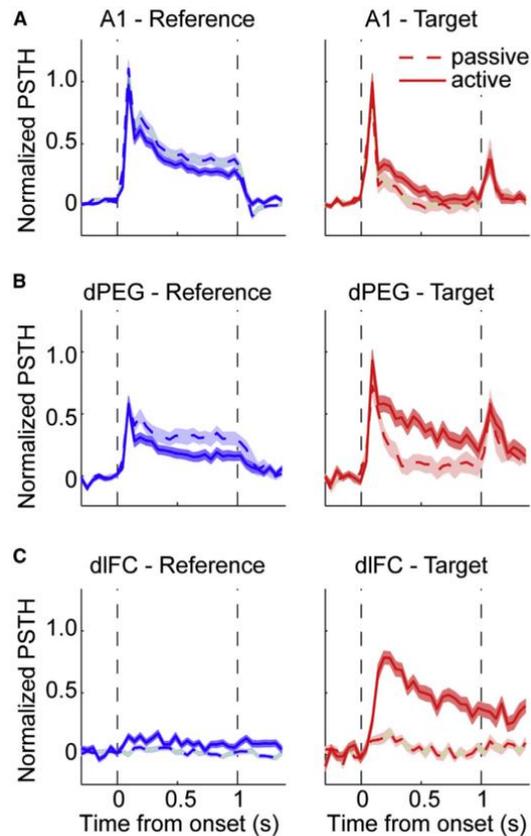


Figure 3.4: Behavior induced plasticity in three areas of auditory processing (A) A1 exhibits slight suppression of reference response during active behavior (B) dPEG appears to have a larger decrease in response to reference stimuli when compared with A1 as well as an increased response to target stimuli (C) dIFC shows little response during passive listening and selects only the target during the active behavioral task (Atiani et al., 2014)

Neurons in A1, on average, showed almost no change in the target response and slight reference suppression. The target enhancement observed in A1 was larger for neurons with a best frequency (BF) within one-quarter of an octave from the tone frequency of the target. However, the neurons of dPEG that showed significant contrast between

target and reference stimuli were those that had a BF within four-fifths of an octave (Atiani et al., 2014). Furthermore, the average responses observed in dPEG showed an increase in sensitivity to the target tone and a decrease in reference responses producing a larger overall contrast between the two. The average dIFC response showed essentially no response to the reference stimuli but exhibited a large sustained response to the target tone during behavior. The rapid task-related response changes largely returned to the baseline patterns in the post-passive stimulus presentation.

3.4 Discussion

The behavioral task used in this study required the animals to quickly recognize a target tone and make the behavioral decision to stop licking from a waterspout to avoid a small shock. Data collected from A1, dPEG, and dIFC under the same behavioral paradigm allowed us to examine the response properties along the auditory processing hierarchy. We see that the representation of the target becomes more prominent as it progresses up through the hierarchy until reaching the executive frontal cortex area where the sound stimulus is represented in essentially a binary manner, present or not present. The secondary auditory cortex appears to be an important step along this pathway as it greatly enhances the selectivity of the target tone and suppresses noisy stimuli that have no behavioral meaning.

This study, expounding on previous studies in primary auditory cortex showing rapid task-related plasticity (J. Fritz et al., 2003), found similar patterns of receptive field changes in dPEG as those observed in A1. However, the response changes from this group of secondary auditory cortex neurons exhibited a relatively greater selective

firing rate increase to the target stimuli during active listening. The target tone enhancement with a similar suppression in reference increased the contrast between the two stimuli. This processing hierarchy of the auditory cortex conforms with the processing hierarchy observed in other sensory cortices previously studied (de Lafuente & Romo, 2006; Kastner & Pinsk, 2004).

3.5 Conclusion

The response properties of dPEG neurons studied here show a blending of functionality observed in A1 and dIFC neurons. The secondary auditory cortex encodes the physical properties of the auditory scene similar to A1. However, as discussed previously, there are differences in the baseline response properties of this auditory area. Additionally, the dPEG neurons exhibited properties similar to dIFC such that there is an enhanced behavioral encoding of the auditory stimuli. The more significant contrast between target and reference sounds in this area enhances the ability of detecting the presence of a target tone. These findings support the idea of secondary auditory cortical areas being an intermediary step between A1 and dIFC and where sound begins to develop meaning.

Chapter 4: Local Field Potential in Auditory Cortical Areas

4.1 Introduction

Previous studies have shown many attention-modulated effects on primary and secondary auditory cortex as well as frontal cortex in the ferret. Much focus has been placed on single unit spike data to examine the response properties and changes for individual neurons and subsequently compiling this information to identify population level effects. Obtaining single unit data requires considerable effort. In addition to the collection of neurophysiological recordings, the data must be spike sorted to get single units and there is a limit to the automation that can be applied to this process. As the number of experiments increases, with a larger number of channels per experiment, the amount of time to sort all this data increases drastically. The intention of this study is to define a method for showing significant effects exhibited by the population of cells within a given cortical area while reducing the level of effort prior to analysis. Local field potential (LFP) offers another potential window into such cortical activity.

4.2 Local field potential

The LFP signal is of growing importance in neurophysiological studies as it is relevant to other common methods of investigation such as electroencephalography (EEG) and magnetoencephalography (MEG) (Kajikawa & Schroeder, 2011). The identification of LFP analysis methods that yield results consistent with single unit data is useful; however, the LFP may provide insight beyond the story that single units can tell as it offers an integrative view for an area of the brain local to the

recording site. Investigations utilizing LFP may possibly lead to new and interesting findings about the effects of behavioral tasks and what happens to basic auditory cortex processing as a sound represents a particular meaning.

The data used in this analysis is from the previously described study regarding secondary auditory plasticity in Chapter Three. In addition to this, local field potential data from primary auditory cortex as well as frontal cortex collected in various other studies (J. B. Fritz et al., 2010; J. Fritz et al., 2003) was used. The data analyzed all come from neurophysiological recordings under the same behavioral task. The LFP is often more difficult to interpret than single unit spikes given the abundance of potential neural sources for the signal (Einevoll, Kayser, Logothetis, & Panzeri, 2013). This study focuses on the power in LFP signals and the changes induced by the pure tone detect behavioral task implemented while collecting this data. Of particular interest is a comparison of behavioral effects between cortical areas.

4.3 Results

4.3.1 Spectrogram Method

The LFP data used in this analysis was averaged across trials, experiments and all animals for a given cortical area. The initial approach to examining the LFP power utilized a nonparametric spectral estimation to visually represent frequencies present in the recorded signal. Given the short duration of target and reference sounds (1 second each) and the temporal response properties previously observed, it is desirable to maintain good temporal resolution (on the order of 100 milliseconds or less). On the other hand, in order to obtain meaningful information from the spectrogram, we

need enough granularity in the spectral resolution (20Hz is used here with multi-taper method) to analyze differences in power for varying frequency bands of the LFP. The standard spectrogram method did not provide this and a multitaper spectrogram was used in its place.

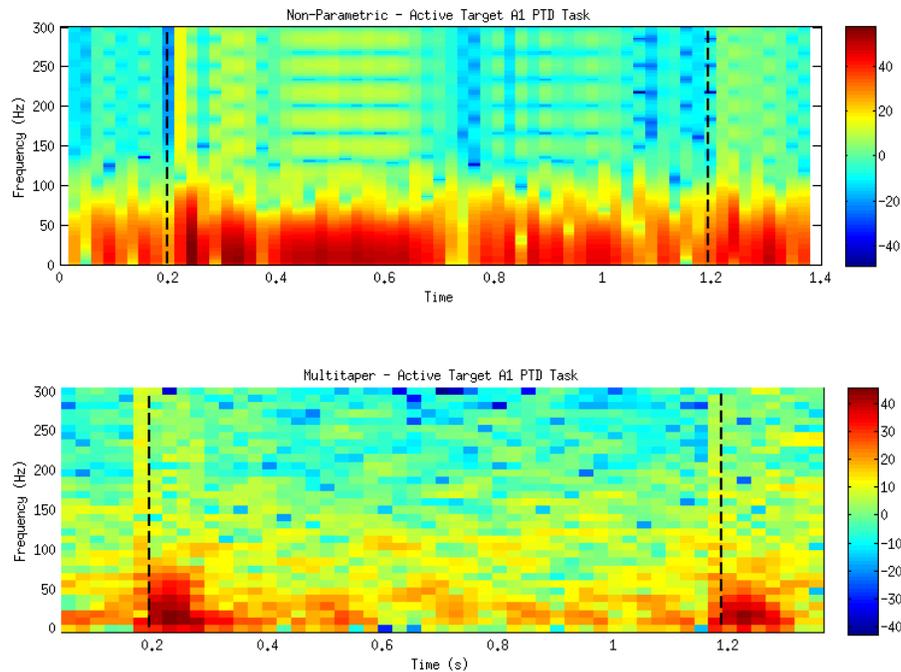


Figure 4.1: (Top) Nonparametric power spectrum analysis of LFP signal shows smearing in time and frequency (Bottom) Multitaper method of nonparametric spectrogram yields “optimal” balance of spectral and temporal resolution. (Dotted black vertical lines indicated stimulus onset and offset)

Multitaper spectrograms offer a nonparametric method for simultaneously addressing bias and variance of the spectral estimation in an “optimal” manner (Babadi & Brown, 2014). The figure below shows the differences in spectrograms produced via these two different methods when examining the same data set from averaged A1 LFP during the pure tone detect auditory task. The multitaper approach allows enough temporal resolution to be obtained without generating the spectral smearing observed when using the non-parametric approach to generating the spectrogram.

Likewise, the multitaper method allows for fine spectral resolution while avoiding temporal smearing.

4.3.2 Behavior Induced Auditory Cortex LFP Power Changes

The power in the LFP signal was examined for each recording area (A1, dPEG, proPPF, and FC) during the various behavioral states of the animals. In order to examine the effect of the behavioral task on LFP power and potential evidence of plasticity in this signal, the pre-passive response has been subtracted from the response recorded during the active pure tone detect task. The reference and target stimulus in the plots below have duration of one second. Additionally, two-tenths of a second silence is plotted pre- and post-stimulus.

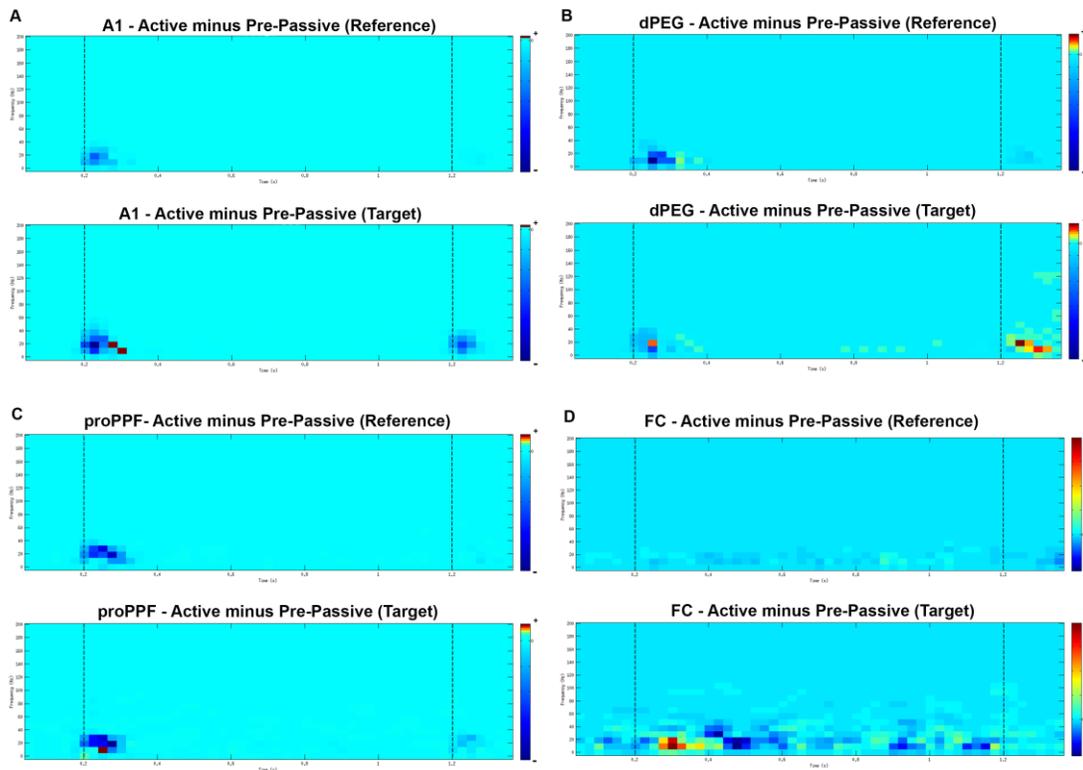


Figure 4.2: Difference between power spectrogram during active and pre-passive stimulus presentation for multiple functional areas with respect to reference and target stimuli

As evident in the difference plots, the most significant change in power occurs in the alpha (8-12Hz) and beta (12-25Hz) bands of the LFP near the onset and offset of the stimulus. Analysis of additional frequency bands, such as gamma (25-100Hz) and high-gamma (100-300Hz), individually did not yield significant changes in the LFP power from pre-passive to active states of the animal. The three auditory areas examined (A1, dPEG, and proPPF) show differences in response to both the reference stimulus as well as the target stimulus. The stimulus onset evokes a difference in the LFP power for reference as well as target sounds. However, the effect of the stimulus offset is more evident when the target tone was presented to the animal. The frontal cortex does not exhibit a significant change between pre-passive and active listening of the reference sounds; although, the change in stimulus onset response is striking when the animal is actively engaged in the behavioral task.

4.4 Discussion

The change in onset response for the reference stimulus in all three auditory areas examined is consistent with previous findings. Likewise the behavioral effect on target stimulus responses was consistent. As would be expected, the frontal cortex did not show any significant change for reference stimuli between the passive and active state of the animal. However, the target tone elicits an increase in power during the active behavioral task. This aligns with the theory that frontal cortex only responds to sounds with meaning such as the target tone during the active behavioral task of the animal. Unfortunately, the LFP power analysis performed here did not yield any novel results but it is consistent with previous findings.

4.5 Conclusion

Various approaches have been utilized in this and other studies in order to abstract meaningful conclusions from the local field potential. Understanding the processing of the pure tone versus noise auditory stimuli used in this study based on neurophysiological recordings is just the first step into understanding the neural processing of a complex auditory scene. The LFP is an information rich signal and future techniques for analyzing this may aid in uncovering population level, attention modulated changes in this auditory processing hierarchy.

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