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# Neural Processes Underlying Auditory Context Effects

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# NEURAL PROCESSES UNDERLYING AUDITORY CONTEXT EFFECTS

By

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# ABSTRACT

## Neural Processes Underlying Auditory Context Effects

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Auditory information within our natural environments is disorganized and often ambiguous, leaving our auditory systems with a complex task: organizing sound into coherent objects. The auditory system uses both current and prior information to assist in completing this task. The influences of previous context on current perception have been referred to as context effects. A *contrastive* context effect results in a current perception that is opposite of what is expected based on the physical stimulus properties presented during an immediate context. A *facilitative* context effect results in a current perception that is the same as the perception during the immediate context. These two context effects were used in the current study to investigate (1) whether they are present during a concurrent sound segregation task (2) whether they arise from the same or different neural processes. Participants completed a concurrent sound segregation task while electrical brain activity was being recorded using electroencephalography (EEG). During the concurrent sound segregation task, participants were presented with sounds and indicated whether they perceived one or two auditory objects, revealing how simultaneous sounds are organized. Behaviorally, results indicated a strong presence of the facilitative effect; however, no contrastive effect was present. Electrophysiologically, results showed no significant contrastive effect and due to an inadequate amount of trials, the facilitative effect was not able to be analyzed. The stimulus parameters used in the current study elicited a strong facilitative effect but no contrastive effect, highlighting a fundamental difference. The specific stimulus parameters used and the resulting outcomes indicate the facilitative effect is more persistent and less susceptible to interference than the contrastive effect.

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# CHAPTER 1

# INTRODUCTION

Sensory information within the real world is constantly changing and often ambiguous, yet our sensory systems can resolve these inconsistencies and produce a coherent and stable perception of our current environment. Our sensory systems use both current and prior sensory information as well as previous experiences to make perceptual decisions about current sensory information. For example, previously listening to a fast speaker will likely result in a subsequent speaker to be perceived as speaking slower than their actual rate. The influences of previous context on current perception have been referred to as context effects.

Two types of context effects have been identified across several modalities (Carter, Konkle, Wang, Hayward, & Moore, 2008; Carter, Snyder, Fung, & Rubin, 2014; Chopin & Mamassian, 2012; Riskey, Parducci, & Beauchamp, 1979; Hulshoff Pol, Hijman, Baare, & van Ree, 1998; Thiel et al., 2014; Huang & Holt, 2012; Kanai & Verstraten, 2005; Snyder, Carter, Lee, Hannon, & Alain, 2008): an effect of prior stimulus (also referred to as adaptation) and an effect of prior perception (also referred to as priming, hysteresis, or perceptual stabilization). The effect of prior stimulus is dependent upon the physical features of the previously presented stimulus (i.e., the context), and is usually contrastive; the perception of the current stimulus (i.e., the test) is opposite of what is expected based on the features of the context. For example, the motion after-effect (MAE) is a contrastive effect found in vision (Addams, 1834). After prolonged exposure to a moving stimulus, a subsequent stationary stimulus appears to be moving in the direction opposite of the moving stimulus. Conversely, the effect of prior perception is dependent upon the perceptual organization of the context, and is usually facilitative; the perception during the test is consistent with the perception during the context. For example, when an ambiguous stimulus (a stimulus that can be perceived in two separate ways) is presented intermittently the perception during the test is the same as the perception during the context.

Context effects are one aspect of how our sensory systems are able to operate efficiently and effectively and they likely have important functions in the real world. The contrastive effect can prepare the system for the uptake of new information, and may assist in adapting to new environments successfully (e.g., adapting to an extremely loud environment such as a concert). The facilitative effect may serve as a mechanism for producing coherent perceptions when faced with ambiguous and incomplete stimuli, and for stabilizing perceptions of an object or person when they move in relation to the observer, or are obstructed by intervening stimuli (e.g., continuing to understand a friends' speech when it is obstructed by ambient noise). Despite the pervasiveness and importance of these context effects, the neural processes underlying them are not fully understood (Carte et al., 2008; Kanai & Verstraten, 2005; Snyder et al., 2008).

A question that researchers have been attempting to answer is what are the neural processes involved with each effect? More specifically, do they arise from one single process (Chopin & Mammassian, 2012; Lages & Treisman, 2010; Noest, 2007; Treisman & Williams, 1984) or two separate processes (Carter et al., 2014; Kanai & Verstraten, 2005; Schwiedrzik et al., 2014) and at what levels of the brain do these processes occur? Studying the processes that underlie these effects provides researchers with a better understanding of how our sensory systems function in order to produce our coherent perceptions of the world. This information is important for improving clinical devices that restore individuals' perceptions (e.g., cochlear implants) and for developing behavioral treatments for individuals living with conditions in which sensory processing is impaired (Alain, Dyson, & Snyder, 2006; Alcantara, Weisblatt, Moore, & Bolton, 2004; Petkov, O'Connor, Benmoshe, Baynes, & Sutter, 2005; Weintraub et al., 2012). It is clear that context effects play a role in efficient sensory processing; therefore, adapting treatments and clinical devices in such a way that utilizes this aspect of processing would prove useful. In addition, by studying these effects across different modalities we are able to detect differences and similarities among them as well as learn more about how the different sensory systems process information. For example, it is possible there are differences in processing specific to each modality, but it is also possible there are general processes contributing to these context effects. Without studying them separately, these processes cannot be identified.

Although context effects have been studied across different modalities (e.g., taste, smell, touch, hearing), they have been studied most extensively in vision. While the research done on visual context effects has certainly contributed to the literature, there still remain unanswered questions about the specific processes involved within other domains and more specifically, in audition. In vision, facilitative and contrastive effects behave in the same predictable way as the context effects found in audition (Chopin & Mammassian, 2012; Gibson & Radner, 1937; Kanai & Verstraten, 2005; Oruc & Barton, 2010). Therefore, drawing on conclusions from the vision literature will be helpful when studying the same effects in an understudied modality, such as audition.

Mostly, these effects have been studied independently and theories of the neural processes responsible for producing the contrastive effect are typically attributed to adaptation within sensory areas. For instance, Huk, Rees, and Heeger (2001) studied the neuronal basis of the motion after effect (MAE) using fMRI (functional magnetic resonance imaging). This contrastive effect is usually attributed to the adaptation of direction-selective neurons. To further test this idea, Huk et al. (2001) conducted an experiment in which they compared brain responses to a test stimulus that either moved in the same direction as the context stimulus or in the opposite direction. The logic was, if adaptation was direction-selective then there should be a weaker response to a test stimulus that is moving in the same direction as the context stimulus; and there should be a stronger response to the test stimulus that is moving in the opposite direction as the context stimulus. Their findings supported this view and they found direction-selective adaptation occurring strongest in areas MT+, V3A, and V4v. Direction-selective adaptation was also found in lower-level areas of the visual system such as V1, V2, and V3 but showed smaller effects relative to the other areas. Area MT+ has been found to be involved in the perception of motion (Albright, 1993) and area V3A has also been found to strongly respond to motion (Smith, Greenlee, Singh, Kraemer, & Hennig, 1998; Tootell et al., 1997). This study suggests that the MAE is attributed to the adaptation of direction-selective neurons which are found in both lower and higher-level areas of the visual system (Huk et al., 2001).

Studies examining the facilitative effect have suggested this effect arises from a form of implicit memory that persists between stimulus presentations (Noest, van Ee, Nijs, & van Wezel, 2007; Wilson, 2007; Sterzer & Rees, 2008; Pearson & Clifford, 2004). However, the areas in which this form of perceptual memory exists is controversial. A study was done to examine what, if any, properties are stored between presentations of a structure from motion stimulus (Chen & He, 2004). Structure from motion is when a rotating 3D stimulus such as a sphere composed of dots linearly moving back and forth, is presented on a screen in two dimensions. The direction of rotation of the 3D stimulus becomes ambiguous. However, when a structure from motion stimulus is presented intermittently, perception stabilizes (i.e., facilitative effect). In this experiment, the researchers changed certain features of the structure from motion stimulus on each presentation such as color, size, and rotation speed. Despite the changing of these features between consecutive presentations, the percept was still stabilized. They explained those certain properties must not have been held in memory since the changing of these features did not disrupt the facilitative effect. The features found to be held in memory are the orientation of the axis around which the stimulus is rotating and visual location (Maier, Wilke, Logothetis, & Leopold, 2003; Chen & He, 2004). When these features changed between stimulus presentations, the facilitative effect did not occur. Considering visual location and orientation are both processed early in the visual hierarchy, these results suggest this implicit memory is sensitive to lower-level characteristics.

Sterzer & Rees (2008) used a binocular rivalry task in which participants were presented with rivalrous stimuli (two separate images presented to each eye) followed by a delay period and then presented with rivalrous stimuli again. Participants were asked to report their perception after each presentation of rivalrous stimuli while their brain activity was being recorded using fMRI. The two rivalrous stimuli used were a female face and a sinusoidal grating. They used the female face stimulus in order to examine a specific area of the brain that shows strong selectivity to certain stimuli in order to better ascertain whether there is implicit memory involved in the facilitative effect. The fusiform face area (FFA) is a region of the brain that has been established to strongly respond to faces; therefore, this was the region of interest when analyzing the data. They reasoned that if there was some type of implicit memory stabilizing the percept during the delay period then they should see increased activity in area FFA when the face percept was stabilized across both rivalrous stimuli presentations. The behavioral results revealed a facilitative effect such that previously perceiving one stimulus type increased the probability of perceiving that same stimulus again. The imaging results showed a significant increase in activity in area FFA during the delay period after participants reported a face percept. They indicated a percept-specific “mnemonic” mechanism involved in the facilitative effect. They also found significant correlations between brain activity in the prefrontal and parietal regions and the tendency to experience perceptual facilitation (Sterzer & Rees, 2008). Taken together, the authors explained the facilitative effect by including the involvement of percept-specific activity in extrastriate visual areas (V3, V4, and MT) as a possible form of implicit memory required for perceptual stabilization. However, it is activity in parietal and pre-frontal regions that aid in deciding whether or not the stored percept enters awareness.

Additional neurophysiological studies have implicated the involvement of frontal and parietal areas during perceptual stabilization (Vernet et al., 2015; Sandberg et al., 2014). For instance, a study used transcranial magnetic stimulation (TMS) during intermittent presentation of ambiguous parallelogram figures that can be perceived as convexed or concaved. TMS uses magnetic stimulation to temporarily disrupt activity in a targeted area of the brain resulting in effects resembling a lesion. When the intraparietal sulcus (IPS) was disrupted about 70ms before the subsequent presentation of the stimulus that had previously been perceptually stabilized, the stabilization was disrupted (Vernet et al., 2015). The authors concluded this brain area is important for stabilizing percepts during intermittent ambiguous stimulus presentations.

In summary, the aforementioned studies investigating the facilitative effect provide evidence for a type of implicit perceptual memory that aids in perceptual stabilization (Noest, van Ee, Nijs, & van Wezel, 2007; Chen & He, 2004; Wilson, 2007; Sterzer & Rees, 2008; Pearson & Clifford, 2004). This implicit memory seems to be stored in areas responsible for processing certain features of the particular stimulus and is sensitive to lower-level characteristics. However, there is also evidence for the additional involvement of higher-order areas (e.g., frontal and parietal) when either deciding which percept will enter awareness (Sterzer & Rees, 2008) or to support the stabilization process (Vernet et al., 2015)

The previously described studies investigated the two context effects separately even though they likely operate simultaneously in the real world. Therefore, it is beneficial to use experimental paradigms that examine both context effects simultaneously while still allowing for them to be analyzed separately. Several studies have used experimental paradigms that achieve this.

In two experiments, Chopin and Mamassian (2012) used binocular rivalry and a tilt after-effect paradigm to investigate whether the two effects arise from the same or different processes. During the binocular rivalry task, participants were first presented with a series of nonrivalrous stimuli (the same stimulus was presented to both eyes) and then were presented with rivalrous stimuli. Participants indicated their perception after the presentation of each rivalrous stimulus. For each reported percept, they looked at what nonrivalrous stimulus was presented directly before (~3 min from the current response) or more distant in the stimulus history (~8 min beginning about 70 stimulus presentations before the current response) to assess the influence of these two time-periods on perception. They found a contrastive effect when analyzing the most recent history and a facilitative effect when analyzing the more distant history. During the tilt after-effect task, participants were presented with a series of stimuli that had one of two orientations followed by an ambiguous test stimulus. Participants indicated which orientation they perceived after the presentation of the test stimulus. Again, they found a contrastive effect when looking at the most recent history and a facilitative effect when looking at the more distant history. The authors explained their results as originating from a single process: predictive adaptation. In predictive adaptation, the visual system is making estimates about the world's statistics using information presented more distant in the past and then generates predictions about the future stimulus using the most recent information. These implicit predictions assume what is being presented in the most recent history should match what has been presented in the more distant history. If a certain proportion of a given stimulus is perceived further in the past, then that same proportion is expected in the most recent history. Increasing the proportion of that same object during the most recent history will make that stimulus less expected (due to adaptation) and therefore less likely to be perceived. Conversely, decreasing the proportion of that same stimulus during the most recent history will make that stimulus expected and therefore more likely to be perceived (Chopin & Mamassian, 2012). When considering relatively longer stimulus history (~ 10 minutes) both the contrastive and facilitative effect can be explained by the proportion of specific stimulus presentations.

In addition to predictive adaptation, criterion setting theory (CST) is another theory that explains these two context effects as arising from a single process (Treisman &Williams, 1984; Lages & Treisman, 2010). This process involves the initial setting of a decision criterion for incoming sensory information based on either previous knowledge, experience, or the initial stimulus. Criterion setting mechanisms then use subsequent information to continually adjust the criterion to optimize perceptual decision making. Based on this theory, context effects are attributed to the shifting of the criterion based on the previous context (Treisman & Williams, 1984; Lages & Treisman, 2010).

Recently, contrastive and facilitative effects were studied using plaid stimuli while simultaneously recording brain activity using electroencephalography (EEG) (Carter et al., 2014). Results show support for separate processes involved with each effect. The plaid stimulus was two superimposed gratings moving at the same speed but in different directions. The angle between the directions of movement of the two gratings can be manipulated to induce perception of a single moving grating, two separate gratings moving in opposite directions, or an ambiguous grating. Trials consisted of a context sequence followed by a test sequence. The context sequence consisted of one of three stimuli: a single plaid stimulus, two separate stimuli, or an ambiguous plaid stimulus. The test sequence always consisted of an ambiguous plaid stimulus. Participants reported their perception after the presentation of each stimulus. Behaviorally, facilitative and contrastive effects were both found. Furthermore, separate event-related potential (ERP) modulations were found specific to both effects. For the contrastive effect, there was a significant linear trend for ERP amplitude to decrease over time during the test, which is contrary to the amplitude increasing over time during the context sequence. In addition, different scalp topographies were found for the processing of the context sequences and test sequences. Low correlations between the angle-related modulations during the context and test sequences were also found. Together, these results indicate that different neuronal populations are involved in the processing of the current stimulus and the contrastive effect. This seems to be contrary to other findings suggesting the contrastive effect occurs within the same areas responsible for processing the features of a particular stimulus. However, this does not rule out the possibility that contrastive effects arise from adaptation of neurons in areas responsible for processing the particular stimulus; this may just be an indication of the involvement of additional brain areas during the contrastive effect. For the facilitative effect, an increased positivity during the test was associated with a segregated percept and unlike the contrastive effect there was a significant correlation between the percept-related brain activity during the context and test. This result suggests common processes involved in the processing of the current stimulus and the facilitative effect and can be taken as evidence for an implicit memory persisting between the context and test. Overall, different electrophysiological findings were present for the contrastive and facilitative effect; thus, providing evidence that these effects arise from different processes.

Auditory context effects have been studied using a sequential stream segregation paradigm that consists of a context period, a silent period, and a test period. Stimuli consist of alternating low and high pitch pure tones where every other high pitch tone is replaced by a silence. The resulting sequence is a repeating ABA- pattern and can be perceived one of two ways. When the frequency separation ($\Delta f$) between the A and B tones is small, it is typically perceived as one coherent stream resembling a galloping rhythm. When the $\Delta f$ is large, it is typically perceived as two separate streams resembling two even metronomes. A sequence with an intermediate $\Delta f$ is ambiguous in which it is possible to hear either one or two streams (Bregman, 1990; Van Noorden, 1975).

Across several studies, using the aforementioned stream segregation paradigm, a contrastive effect of prior stimulus was found such that being presented with a small $\Delta f$ during the context resulted in a higher proportion of two stream percepts during the test and vice versa when a large $\Delta f$ was presented during the context. A facilitative effect was also found when both the context and test consisted of ambiguous sequences such that the perception during the context (i.e., either one or two streams) persisted during the test (Snyder et al., 2008; Snyder, Carter, Hannon, & Alain, 2009a; Snyder, Holder, Weintraub, Carter, & Alain, 2009b; Snyder & Weintraub, 2011; Snyder & Weintraub, 2013). In a follow up study, Snyder et al. (2009a) used sequences with different frequency ranges during the context and test and although reduced, still found a contrastive effect. This finding suggests that this effect may arise from the adaptation of neurons in auditory cortex that are widely tuned to frequency information.

Furthermore, Snyder et al. (2009b) recorded brain activity using EEG while participants completed the previously described stream segregation task. They found different neural modulations and scalp topographies associated with each effect, suggesting different processes. For the contrastive effect, the ERPs elicited during the test consisted of a decreased P1 (~ 80-90 ms post stimulus onset) amplitude as the $\Delta f$ during the context increased. This early modulation might be indicative of adaptation occurring in lower-level sensory areas. For the facilitative effect, there was a positive modulation during the test occurring at the beginning of a tone sequence associated with the stabilization of a two-object percept. This modulation might be indicative of some form of implicit memory or sustained response that continues to bias perception through the silent interval between the context and test.

Taken together, there are studies suggesting that both effects arise from one single process (Chopin & Mamassian, 2012; Treisman & Williams, 1984; Lages & Treisman, 2010) while others claim these effects arise from two separate processes (Carter et al., 2014; Kanai & Verstraten, 2005; Schwiedrzik et al., 2014; Snyder et al., 2009b). Furthermore, there are studies claiming the involvement of adaptation of neurons responsible for processing certain features of a particular stimulus in lower-level areas with the contrastive effect (Huk et al., 2001; Kanai & Verstraten, 2005; Schwiedrzik et al., 2014; Snyder et al., 2009a) while higher-level areas are involved with the facilitative effect (Kanai & Verstraten, 2005; Schwiedrzik et al., 2014; Sterzer & Rees, 2008; Vernet et al., 2015). Conversely, there are also studies claiming the facilitative effect involves lower-level sensory areas (Chen & He, 2004; Chopin & Mamassian, 2012; Pearson & Clifford, 2004; Sterzer & Rees, 2008). In summary, the phenomena of context effects and the neural processes involved are conflicting and not fully understood.

# CHAPTER 2

# CURRENT STUDY

The current study will use an auditory scene analysis (ASA) task (mistuned harmonic segregation) to investigate context effects in audition. Auditory scene analysis (ASA) is the process of organizing acoustic information within our environment into meaningful objects, resulting in our coherent perceptions of sound (Bregman, 1990). Scientists study ASA in order to reach a better understanding of how the auditory system functions. Context effects likely have important functions related to ASA, and sensory processing in general. Therefore, researching auditory context effects using an ASA task will contribute to the literature on ASA as well as to the literature on context effects, thus providing knowledge about auditory processing and sensory processing in general. The stream segregation paradigm used in the studies conducted by Snyder and colleagues is also an ASA task. That paradigm simultaneously investigated the *sequential* organization of sounds and auditory context effects. These tasks typically use longer stimulus sequences in order to evaluate how sensory information is organized over time. For instance, sequential organization is necessary for identifying the melody of a particular song. The task in the current study will investigate the *concurrent* organization of sounds while simultaneously investigating context effects. These tasks typically involve the presentation of multiple sounds that overlap in space and time in order to investigate how simultaneous sound sources are organized into distinct objects. For instance, concurrent organization is necessary for being able to distinguish between simultaneous speakers at a dinner party.

The current study has three aims. The first is to determine if context effects are present during a mistuned harmonic segregation task (Alain, Arnott, & Picton, 2001; Hartmann, McAdams, & Smith, 1990; Moore, Glasberg, & Peters, 1986). The second is to identify the neural processes associated with each context effect. The third is to investigate whether these effects arise from the same or different neural processes. The current study used a mistuned harmonic segregation task and was structured such that trials consisted of a context stimulus, a silence, and a test stimulus. The stimuli used were 400 ms harmonic complex tones. The physical structure of the complex tones was manipulated in one of three ways: to induce a perception of one auditory object (i.e., tuned), two auditory objects (i.e., mistuned), or to induce a perception where it was equally likely to perceive one or two objects (i.e., ambiguous). Throughout the experiment, the context contained all three manipulations while the test contained only the ambiguous complex tone. After the presentation of each sound, participants indicated whether they heard the stimulus as “tuned” or “mistuned”. Participants performed this behavioral task while simultaneously recording brain activity using EEG. This allowed for the investigation of whether these effects were present during a mistuned harmonic segregation task, what neural mechanisms were associated with each effect, and whether these effects arise from the same or different processes.

EEG is a useful tool when researching the underlying processes associated with the processing of a certain stimulus, or phenomenon. Although EEG does not have the same source localization abilities as other brain imaging techniques such as fMRI, it does have superior temporal precision, and source localization techniques are available to apply to EEG data. Precise temporal information can provide information about where certain processes are taking place within the brain, in addition to when. For example, it is generally considered that neural activity occurring earlier in time is indicative of lower-level processes while activity occurring later is indicative of higher-level processes (Luck, 2005; Luck, 2012). The precise timing of EEG is also useful for identifying components that are fundamental to a certain process or task. Once these components are identified they can be examined for differences due to experimental manipulations.

ERP components fundamental to mistuned harmonic segregation have been identified through research done by Alain and colleagues and will help to guide this current study. In these studies, they used harmonic complex tones that were manipulated as to induce either a tuned or mistuned percept while recording brain activity using EEG. Isolating the differences between two conditions is best illustrated through calculating difference waves. For example, subtracting neural activity associated with a one-object percept from neural activity associated with a two-object percept will leave only the difference in activity between the two conditions. Through several experiments, Alain and colleagues have found two components referred to as the object-related negativity (ORN) and the P400 through calculating difference waves (Alain et al. 2001, Alain, Schuler, & McDonald, 2002; Alain, Theunissen, Chevalier, Batty, & Taylor, 2003, Alain & Izenberg, 2003). The ORN is an increased negativity around 140 ms post stimulus onset, is maximal at frontocentral sites and reverses in polarity at inferior temporal sites. This reversal pattern suggests neural generators in or around the primary auditory cortex and source localization techniques have provided further support for this claim (Alain et al. 2001; Alain et al. 2003; Arnott, Bardouille, Bernhard, & Alain, 2011). This is consistent with other research providing evidence for the role of primary auditory cortex in the segregation of concurrent auditory stimuli (Alain, 2007; Bidet-Caulet, Fischer, Bauchet, Aguera, & Bertrand, 2007). The putative location, along with the presence of the ORN during both active and passive listening, and when competing tasks are being performed, suggests a somewhat automatic process related to concurrent sound segregation that physically evaluates the structure of the stimulus (Alain et al., 2001; Alain et al., 2002; Alain & Izenberg, 2003; Dyson, Alain, & He, 2005). The P400 is an increased positivity around 350 ms poststimulus onset, is maximal at frontocentral cites and reverses in polarity at occipital and temporal sites (Alain et al. 2001, Alain et al., 2002). It is also thought to be an index of concurrent sound segregation, increasing in amplitude with larger mistuning percentages, but unlike the ORN, it is only present when participants are asked to make perceptual judgments (Alain et al. 2001; Alain et al., 2002). The P400 has a scalp distribution that is more widespread relative to the ORN and reverses in polarity between frontocentral and occipital and temporal sites suggest generators in auditory association cortices and the temporal lobe (Alain et al., 2001). The P400 has been posited to reflect more controlled processes, that occur higher up in the hierarchy of the auditory system, that evaluate whether there is more than one object present (Alain et al., 2001; Alain et al., 2002). These components served as a starting point for ascertaining what neural processes were associated with the context effects within a mistuned harmonic segregation task.

# CHAPTER 3

# METHODOLOGY

## Participants

Thirty normal-hearing adults (<30 dB HL from 250 to 8000 Hz, 19 female, age range = 18-27 years, mean age = 21.96) from the University of Nevada, Las Vegas and the Las Vegas community participated after giving written informed consent according to the guidelines of the University's office for the Protection of Research Subjects. A total of four participants were excluded from the final analysis for excessive artifacts in the EEG recordings, defined as retention of less than 40% of the trials in the analysis.

## Stimuli

Auditory stimuli were generated off-line in Matlab (The MathWorks, Inc., Natick, MA) and consisted of complex sounds with a fundamental frequency ($f_0$) of 200 Hz comprised of five pure tones at equal intensity (400 ms in duration, including 5 ms rise/fall times). Figure 1 depicts the structure of the complex tones. The sounds were presented binaurally through ER3A headphones (Etymotic Research, Inc., Elk Grove Village, IL) at around 65 dB sound pressure level (SPL). Stimuli were presented and behavioral responses were collected by a custom program written in Presentation (Neurobehavioral Systems, Inc., Albany, CA), running on a Pentium 4 computer with a SB X-Fi sound card (Creative Technology, Ltd.). Behavioral responses were collected on a RB-830 response box (Cedrus Corporation, San Pedro, CA).

## Procedure

Each trial consisted of a 400 ms *context stimulus* and a 400 ms *test stimulus*, with a 2 s silent duration between the two tones. The intertrial interval was 2 s. Context stimuli consisted of

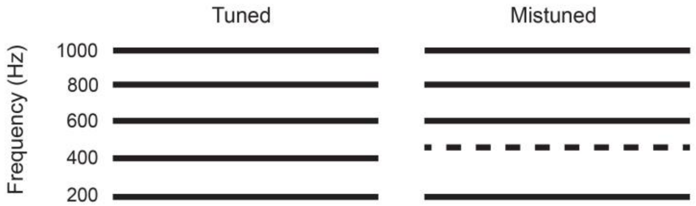

Figure 1. Structure of stimuli used in the current study. Harmonic complex tones consisted of 5 harmonics with a fundamental frequency of 200 Hz. Stimuli were either tuned (left) in which each harmonic was an integer multiple of the fundamental (200 Hz) or mistuned in which the second harmonic was mistuned upwards by either 2% (408 Hz) or 16% (464 Hz).

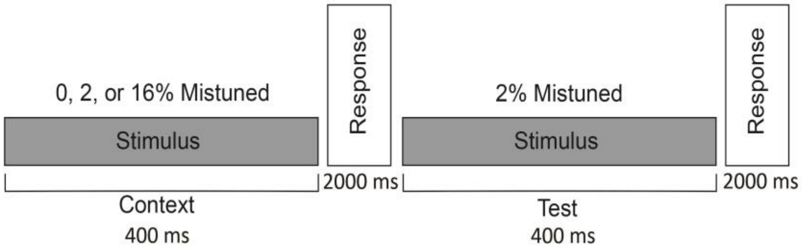

Figure 2. Example of an experimental trial. Each trial consisted of a 400 ms context tone that was mistuned by 0, 2, or %16, a 2000 ms inter-stimulus interval, a 400 ms test stimulus that was mistuned at a constant 2% and then a 2000 ms inter-trial interval. After the presentation of each stimulus participants indicated whether their perception was tuned or mistuned.

a 400 ms complex sound that was either "tuned" in which all the harmonics were an integer multiple of the $f_0$ of 200 Hz or "mistuned" in which the second harmonic differed from 400 Hz upwards by 2% (408 Hz) or 16% (464 Hz) of its original value. Test stimuli always consisted of a mistuned complex sound in which the second harmonic was mistuned upwards by 2% (408 Hz) of its original value. Figure 2 depicts the structure of the experimental trials. Based on a pilot study that was previously conducted, the

2% mistuning percentage lead to an ambiguous percept in which it is possible to either hear out the mistuned harmonic or perceive it as tuned. By keeping the test at a constant ambiguous mistuning percentage, any changes in response to the stimuli can be attributed to the manipulation during the context. Additionally, effects of context are most prominent when the stimulus characteristics of the test are not biased as to induce a particular percept (e.g., ambiguous stimuli).

During both the context and test participants were instructed to listen to the sounds and make perceptual judgments based on how they heard the sounds. Tuned stimuli were described to participants as sounding “buzzy” in which only one auditory object was present and mistuned stimuli were described as sounding “buzzy and beepy” in which two auditory objects were present. Participants were told to press one button on the response box if they heard the sound as “buzzy” (i.e., tuned) and to press another button on the response box if they heard the sound as “buzzy and beepy” (i.e., mistuned). Participants were played examples of both tuned and mistuned stimuli prior to the experiment to ensure they could perceptually differentiate the two sounds. Next, participants completed 12 practice trials that also consisted of a context and test stimulus but included variations of tone duration and mistuning percentage during the context that differed from experimental trials. The mistuning percentage of the test stimulus remained the same as experimental trials (2%). Participants were not explicitly told there were context and test periods, instead they were told to respond after the presentation of each sound, and to let their perception take a natural course. In total, the experiment consisted of 600 trials, 200 for each mistuning percentage during the context (0, 2 and 16%), and were broken up into eight separate blocks comprised of 75 trials each. Trials were randomized within blocks. Participants were seated in a sound-attenuated booth (Industrial Acoustics Corp., Bronx, NY) and were asked to maintain fixation on a white cross on a black background in the center of the computer screen throughout the experiment. They were also asked to refrain from any bodily movements including their eyes and head while stimuli were being presented.

**Electrophysiological Recording.** Electroencephalographic (EEG) signals were digitized continuously using a Biosemi ActiveTwo system (http://www.biosemi.com). The EEG was recorded from an array of 72 electrodes, with a Common Mode Sense (CMS) active electrode and Driven Right Leg (DRL) passive electrode serving as ground and re-referenced to the average of all electrodes (see http://www.biosemi.com/faq/cms&drl.htm), placed at 64 points based on the 10/20 system in a Biosemi electrode cap and 8 additional points below the hairline (both mastoids, both pre-auricular points, outer canthus of each eye, and inferior orbit of each eye) and were recorded on to a PC desktop computer for off-line analysis. Before EEG recording, conducting gel was applied to the skin at each electrode site with the cap on and sintered Ag-AgCl pin type electrodes were fitted into place at each site in the cap. Electrodes were attached to eight sites below the hair line. Voltage offsets were below 40µV prior to recording, and the resting EEG was checked for any problematic electrodes prior to and throughout the recording session.

**Behavioral Analyses.** Two behavioral analyses were conducted; one that examined the effect of mistuning during the context and another that examined the two context effects. To look at the effect of mistuning during the context, the proportion heard as mistuned was calculated for each mistuning percentage (0, 2 and 16%) and resulting values were entered into a one-way repeated-measures ANOVA to reveal any differences in behavioral responses during the context as a function of mistuning percentage.  To examine the two context effects, behavioral data was first organized into two separate groups based on whether the context was perceived as tuned or mistuned. Within those two groups, the proportion heard as mistuned during the test was calculated for each participant and for each mistuning percentage presented during the context (0, 2 and 16%). The resulting values were entered into a 2 (perception during the context) x 3 (mistuning percentage during the context) repeated-measures ANOVA to reveal any differences in the proportion heard as mistuned during the test as a function of both perception and mistuning percentage during the context. When there was more than one level present in an ANOVA, the degrees of freedom were adjusted with the Greenhouse-Geisser epsilon (ε) and all reported probability estimates were based on the reduced degrees of freedom.

**Electrophysiology Analyses.** All off-line ERP analyses were performed using Brain Electrical Source Analysis software (BESA; MEGIS Software GmbH, Grafelfing, Germany). Noisy electrodes were interpolated prior to analysis. Ocular artifacts (blinks, saccades and smooth movements) were corrected automatically with a spatial-filtering-based method (Ille, Berg, & Scherg, 2002). Epochs contaminated by artifacts (amplitude > 120 μV, gradient > 75 μV, low signal < 0.01 μV) were automatically rejected before averaging. EEG epochs were averaged separately across all non-artifact trials for each of the ten different ERPs of interest, for each electrode site, and re-referenced to the average of all electrodes not adjacent to the eyes. The ERPs of interest were those elicited during the context and corresponding test for each separate mistuning percentage (0, 2 and 16%) and those elicited during the context and test when the tone was perceived as tuned and mistuned only for conditions where the mistuning percentage was 2%. Epochs began 500ms before stimulus onset and continued for 1000ms. ERP averages were baseline corrected by subtracting the average of the 100ms pre-stimulus period from each point in the entire epoch. Epochs were digitally bandpass filtered to attenuate frequencies below 0.01 Hz (6dB/octave attenuation, forward) and above 30 Hz (24dB/octave attenuation, zero phase). The ERPs of interest were averaged across all participants and were quantified by calculating the mean amplitude in selected latency regions relative to the 100 ms baseline activity.

Difference waves were also computed in which the ERP elicited during one trial type was subtracted from the ERP elicited during a different trial type. Difference waves are especially useful when attempting to isolate differences in neural activity between two conditions and for isolating ERP components that are fundamentally associated with a certain task or process. Difference waves were calculated to look at the effects of current mistuning (16% Context – 0% Context), current perception (Mistuned Percept – Tuned Percept), prior mistuning (0% Test – 16% Test), and prior perception (Mistuned Percept – Tuned Percept).

Lastly, overall strength of neural activity and dissimilarity of scalp configurations across epochs were calculated. The overall strength of neural activity across time points for each condition of interest is indexed by calculating global field power (GFP). This was done by calculating the standard deviation of the voltage across all electrodes at each time point for each participant. The resulting values were then averaged across subjects and specified time ranges were compared between conditions. The ORN (125-210 ms) and P400 (350-420 ms) time ranges were used during the context and the resulting values were entered into a one-way repeated measures ANOVA to test for differences in overall strength between the three mistuning percentages (0, 2, and 16). The ORN (105-170 ms) time range during the test was used to investigate differences in overall strength as a function of mistuning percentage during the test. The resulting values were entered into a one-way repeated measures ANOVA. The dissimilarity of scalp configurations between conditions of interest are indexed by calculating global map dissimilarity (GMD). This was done by computing the standard deviation between successive topographies considering all possible electrodes across each time point within a given epoch (e.g., global dissimilarity for topography (1) and topography (2), topography (2) and topography (3), etc.) irrespective of the strength of neural activity. More specifically, where are the maxima and minima voltages distributed within a given topography and how does the spatial distribution of these voltages differ between each time point. The resulting values are then averaged across subjects and compared between conditions (Context 0 vs. Context 2, Context 0 vs. Context 16, Context 2 vs. Context 16, Test 0 vs. Test 2, Test 0 vs. Test 16, Test 2 vs. Test 16). This analysis was completed using Cartool and the resulting dissimilarity values range from 0 (no difference) to 2 (topographic inversion). A non-parametric randomization test was used to test for statistically significant topographical differences at each time point and were indexed by a value of less than .05. The computation done during the statistical test was as follows: (1) randomly assigning the topography maps of subjects into different groups, (2) averaging the new groups ERP's, (3) recalculating the GMD values. This procedure is repeated a number of times, $2^n$, where '*n'* is the total number of subjects, and the GMD values from each permutation are compared to the GMD values from the actual data to assess the probability that the GMD values from the randomization procedure are higher than the actual GMD values. Traditional ERP analyses include selecting subsets of electrodes and computing mean amplitudes or latencies in specified time ranges that are reference dependent. GFP and GMD are reference free analyses that take into account all electrodes simultaneously, thus revealing an unambiguous measure of potential field strength and dissimilarity of scalp configurations across time (Lehmann & Skrandies, 1980). Using these two analyses in conjunction can provide insight as to whether conditions are differing only in overall neural strength or if they also differ in scalp configurations.

# CHAPTER 4

# RESULTS

## Behavioral Results

In line with previous research, a one-way repeated measures ANOVA revealed larger mistuning percentages during the context resulted in greater amounts of mistuned percepts, *F* (2,50) = 70.33, $p < .001$, $\eta_p^2 = .74$ (Alain et al., 2001; Moore et al., 1986; Hartmann et al., 1990). The 2 (prior perception) x 3 (prior mistuning) repeated-measures ANOVA was computed to investigate the effect of prior mistuning, the effect of prior perception, and any interactions that

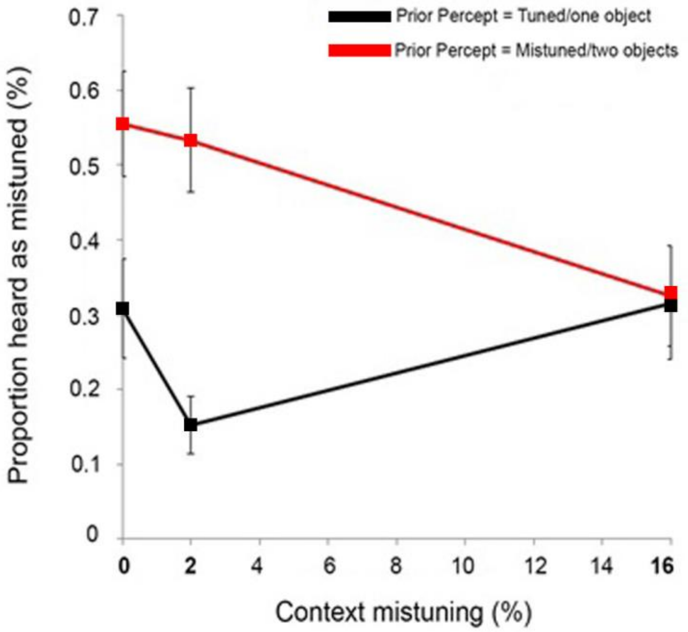

Figure 3. Behavioral results for the effect of prior mistuning and prior perception. The proportion heard as mistuned during the test for each mistuning percentage during the context and for each prior percept. Red line depicts the effect of prior mistuning when the context was perceived as tuned and the black line depicts the effect of prior mistuning when the context was perceived as mistuned. The effect of prior perception is evident by the distance between the red and black lines during the 2% context mistuning.

may be present. There was a non-significant main effect of prior mistuning, $F$ (2,38) = 2.93, $p$ = .076, $\eta_p^2 = .13$, with a trend for more perception of two objects with smaller prior mistuning. There was a significant effect of prior perception, $F$ (1,19) = 20.25, $p < .001$, $\eta_p^2 = .52$, such that there was a greater likelihood that the ambiguous test stimulus was perceived as mistuned when the context stimulus was perceived as mistuned and vice versa when the context stimulus was perceived as tuned (facilitative) for the 0 and 2% mistuning conditions. Lastly, results showed a significant interaction, $F$ (2,38) = 16.92, $p < .001$, $\eta_p^2 = .47$. These results are plotted in Figure 3. The significant interaction revealed that the effect of prior perception was largest when the context mistuning was 2%, $F$ (1,27) = 56.48, $p < .001$, $\eta_p^2 = .68$, relative to when the context mistuning was 0%, $F$ (1,27) = 12.69, $p < .001$, $\eta_p^2 = .32$, and not present during the 16% context mistuning condition, $F$ (1,25) = .08, $p = .75$, $\eta_p^2 = .003$. However, I was mostly interested in the effect of prior perception when the context and test mistuning were 2%. I will not further speculate about the presence of a facilitative effect for the 0% mistuning condition and the lack of effect during the 16% context condition. Additionally, there were very little two object percepts during the 0% context and very little one object percepts during the 16% context so it is possible that these effects or lack thereof are merely artifacts of extremely uneven amounts of trials.

### Event-Related Potential Data

**Waveform Analyses.** Figure 4 presents the grand average ERP waveforms elicited by 0, 2 and 16% mistunings during the context and the scalp topography of the difference wave (16% - 0%) during the ORN time range. The ERPs elicited during the context for each trial type (0, 2 and 16%) were averaged separately and entered into a one-way repeated measures ANOVA to test for differences in ERP amplitude during the ORN and P400 time ranges. Figure 5 shows the mean amplitude for each mistuning percentage presented during the context for the ORN and P400 time ranges. The ANOVA during the ORN time range (125-210 ms) using electrodes Fcz, Fz, F1, F2, Fc1 and Fc2 replicated previous findings such that larger mistuning percentages elicit greater amplitudes, $F\ (2,50) = 6.25$, $p < .005$, $\eta_p^2 = .2$ (Alain et al. 2001; Alain et al. 2002). Post-hoc paired-samples t-test's revealed greater negative amplitudes during the 16% mistuning condition when compared to the 0%, $t\ (25) = 3.34$, $p < .01$, and the 2% conditions, $t\ (25) = 2.32$, $p < .05$. However, there was no amplitude difference between the 0% and 2% conditions, $t\ (25) = .37$, $p = .71$. The ANOVA during the P400 time range (350-420 ms) using electrodes Fcz, Cz, Fc1, Fc2, Cz and C2 also replicated previous findings such that greater mistuning percentages elicited greater amplitudes, $F\ (2,50) = 12.29$, $p < .001$, $\eta_p^2 = .33$ (Alain et al. 2001; Alain et al. 2002). Post-hoc paired-samples t-test's revealed greater positive amplitudes during the 16% mistuning condition when compared to the 0%, $t\ (25) = -3.59$, $p < .001$, and the 2% conditions, $t\ (25) = -3.64$, $p < .001$. Again, there was no amplitude difference between the 0% and 2% conditions, $t\ (25) = -.79$, $p = .44$.

The ERPs elicited during the test for each mistuning percentage presented during the context (0, 2 and 16%) were averaged separately across all participants. The resulting ERPs are depicted in Figure 6. Mean amplitude was calculated during the ORN time range (105-170 ms) using electrodes Fcz, Fz, Cz, Fc1 and C1 and during the time range where a late difference appeared (520-620 ms) using electrodes F1, Fc1, Fc2, Fz, F2 and Fcz for each condition (0, 2 and 16%). Resulting values were entered into a one-way repeated measures ANOVA to test for differences in ERP amplitude during the test as a function of mistuning percentage during the context. Figure 7 shows the mean amplitude for the ORN time range during the test for each mistuning percentage presented during the context. Although the effect of prior mistuning during the ORN time range was not significant, $F$ (2,50) = 3.11, $p$ = .058, $\eta_p^2$ = .11, the 16% mistuning condition did elicit quantitatively smaller amplitudes during the test (M = -1.04) relative to the 2% (M = -1.28) and 0% conditions (M = -1.23). This result, albeit statistically insignificant, indicates there is some adaptation occurring within auditory cortex. Given, that there is no behavioral contrastive effect could mean this possible adaptation occurring in primary auditory cortex is not sufficient to influence perceptual processes. The late difference also revealed no significant differences between conditions, $F$ (2,50) = 2.4, $p$ = .11, $\eta_p^2$ = .426.

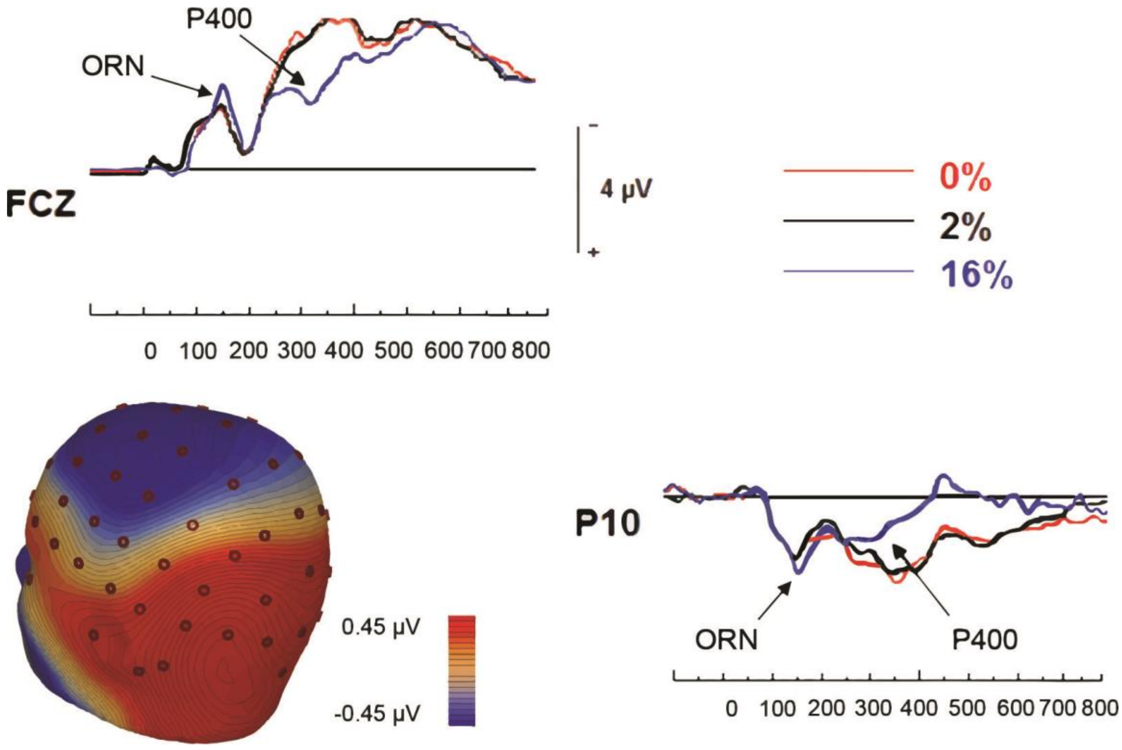

Figure 4. Electrophysiological data elicited during the context for 0, 2 and 16% mistunings. ORN and P400 were most prominent at frontocentral electrodes and reversed polarity at parietal electrodes. ORN and P400 amplitudes increased with greater mistuning percentage. Scalp topography shown during as the difference between the 16 and 0% mistunings during the ORN time range (~ 135 ms).

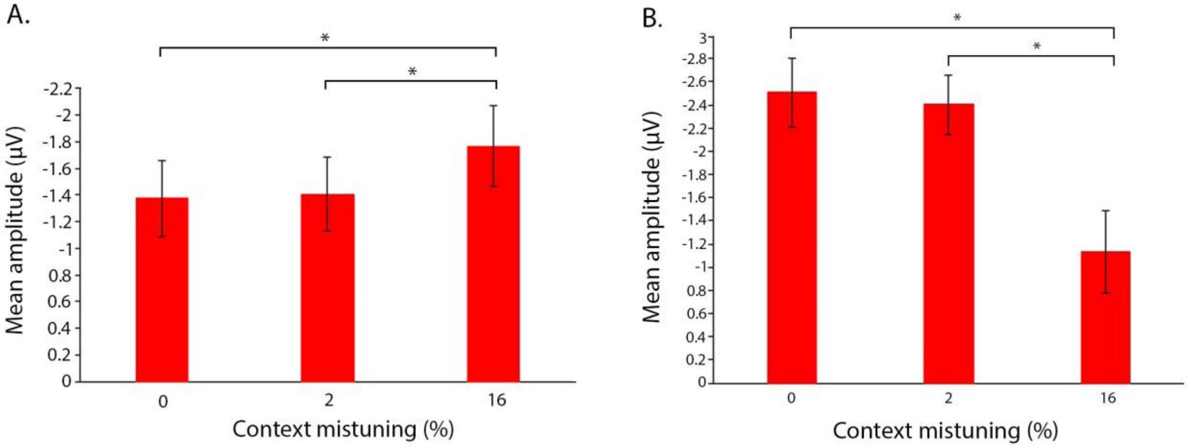

Figure 5. (A) calculated mean amplitude during ORN time range (125 – 210 ms) during the context for each mistuning percentage. (B) calculated mean amplitude during P400 time range (350 – 420 ms) during the context for each mistuning percentage. Significant differences between conditions are denoted by asterisks.

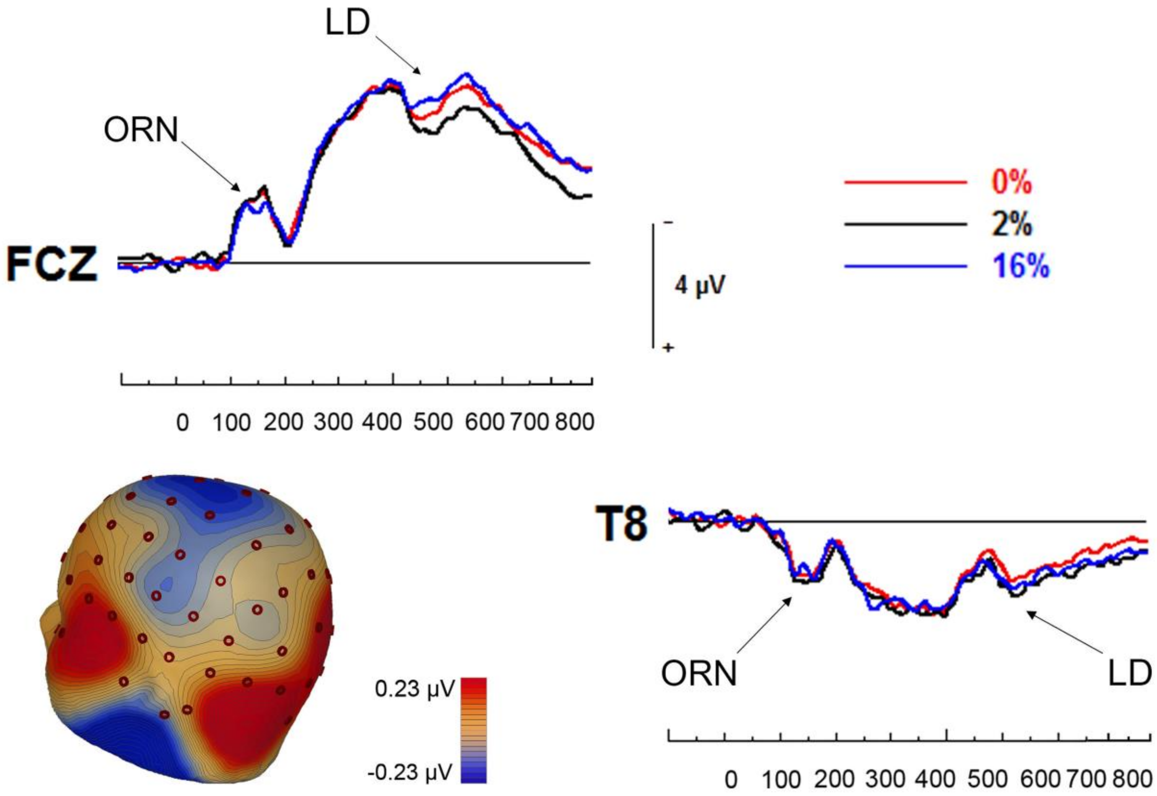

Figure 6. Electrophysiological data elicited during the test for 0, 2 and 16% mistunings. ORN and was most prominent at frontocentral electrodes and reversed polarity at temporal electrodes. Additionally, a late difference (LD) emerged around 520 ms and reversed polarity at temporal electrodes. Scalp topography shown as the difference between the 0% and 16% mistunings during the ORN time range (~ 135 ms).

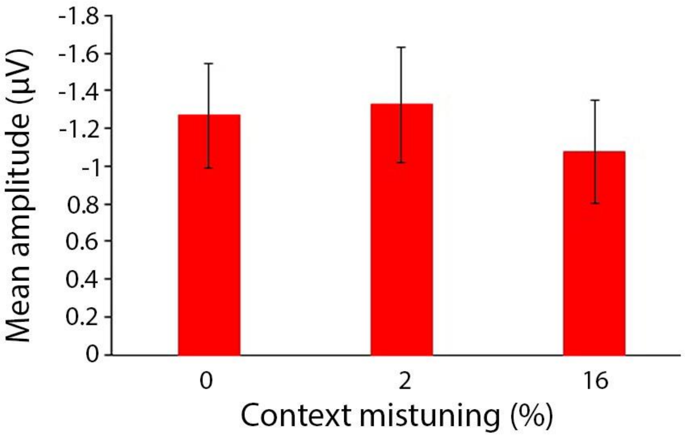

Figure 7. Calculated mean amplitude during ORN time range (105 – 170 ms) during the test for each mistuning percentage presented during the context. Results revealed no significant differences.

To examine the effect of current perception, the ERPs elicited during the context for tuned and mistuned percepts were averaged separately. Only conditions in which the context was mistuned by the ambiguous 2% were analyzed in order to examine the effects of current perception while controlling for any confounding physical stimulus differences. To examine the effect of prior perception, the ERPs elicited during the test when the context was perceived as tuned and mistuned were averaged separately. Only conditions in which the context and test were both mistuned by the ambiguous 2% were analyzed. Due to an extremely uneven amount of one object and two object responses, the electrophysiological data related to the effect of current and prior perception were not further statistically analyzed. It is important to have sufficient trials when statistically analyzing event-related potential data to reliably remove artifacts and other noise from the signal. The paucity of two object responses rendered the current and prior two object conditions extremely noisy. Therefore, I did not feel reliable or valid interpretations --relating to the effect of current and prior perception--could be made.

**Global Field Power Analyses.** In addition to the traditional event-related potential analyses (i.e., computing mean amplitudes), I computed the overall strength of neural activity across all electrodes within the ORN time range (125-210 ms) separately for each condition (Context 0, 2 and 16%, Test 0, 2 and 16%) and during the P400 time range (350-420 ms) only for the context conditions (0, 2 and 16%) (Alain et al., 2001). Results indicated a significant effect of context mistuning, $F$ (2,50) = 6.82, $p < .01$, $\eta_p^2 = .21$ during the ORN time range. Post-hoc paired-samples t-test's revealed greater overall strength of neural activity during the 16% mistuning condition when compared to the 0%, $t$ (25) = -4.02, $p < .001$, and the 2% conditions, $t$ (25) = -2.42, $p < .05$. However, there was no difference in overall strength of neural activity between the 0% and 2% conditions, $t$ (25) = -.42, $p = .68$. This aligns with the traditional ERP results showing greater amplitudes during the 16% context condition when compared to the 0% and 2% conditions and the lack of difference in mean amplitude between the 0% and 2% mistuning conditions. The greater strength in neural activity during the 16% condition could reflect a mismatching process based on the physical stimulus between the expected harmonic template derived from the first two harmonics and the mistuned third harmonic. The lack of difference between the 0% and 2% conditions might be because the mistuning percentage of 2% is too small to elicit a strong mismatch. When investigating the differences in overall neural strength between the 0, 2 and 16% context mistunings during the P400 time range (350-420 ms) results revealed no significant effects, $F$ (2,50) = 1.6, $p$ = .21, $\eta_p^2$ = .06. Lastly, there were no significant effects of GFP during the test within the ORN time range (105-170 ms), $F$ (2,50) = 1.21, $p$ = .3, $\eta_p^2$ = .05. Lastly, GFP analyses were computed during the test within the time range of the late difference and the results were not significant, $F$ (2,50) = 1.46, $p$ = .24, $\eta_p^2$ = .24. GFP values are plotted in Figure 8.

**Global Map Dissimilarity Analyses.** The topographic dissimilarities between conditions at successive time points were calculated and the results during the context are plotted in Figure 9 while the results for the test are plotted in Figure 10. There were no significant topographic dissimilarities in the ORN or P400 time ranges when comparing the 0% and 2% mistuning conditions. There were significant topographical differences during the P400 time range when comparing the 0% and 16% mistuning conditions and when comparing the 2% and 16% mistuning conditions. This might be reflective of the recruitment of additional brain areas when making perceptual decisions and when the current percept is two objects. This explanation coincides with results from a study that used fMRI to further elucidate the neural substrates involved with sequential stream segregation. They found activity within the intraparietal sulcus when participants perceived an ambiguous tone sequence as two streams (Cusack, 2005). There were no significant GMD results during the test.

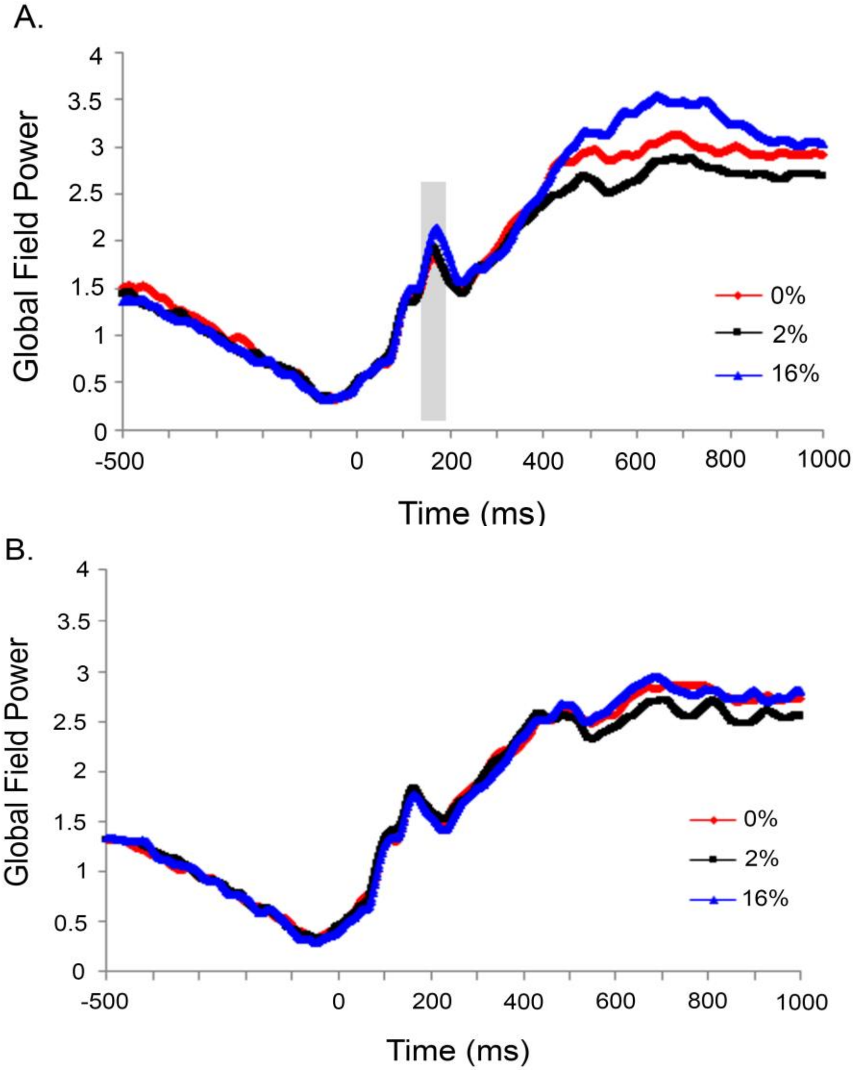

Figure 8. (A) Context GFP depicted for each mistuning percentage. Significant differences in GFP are present during the ORN time range (105-170 ms). (B) Test GFP depicted for each mistuning percentage presented during the test. There were no significant differences during the test.

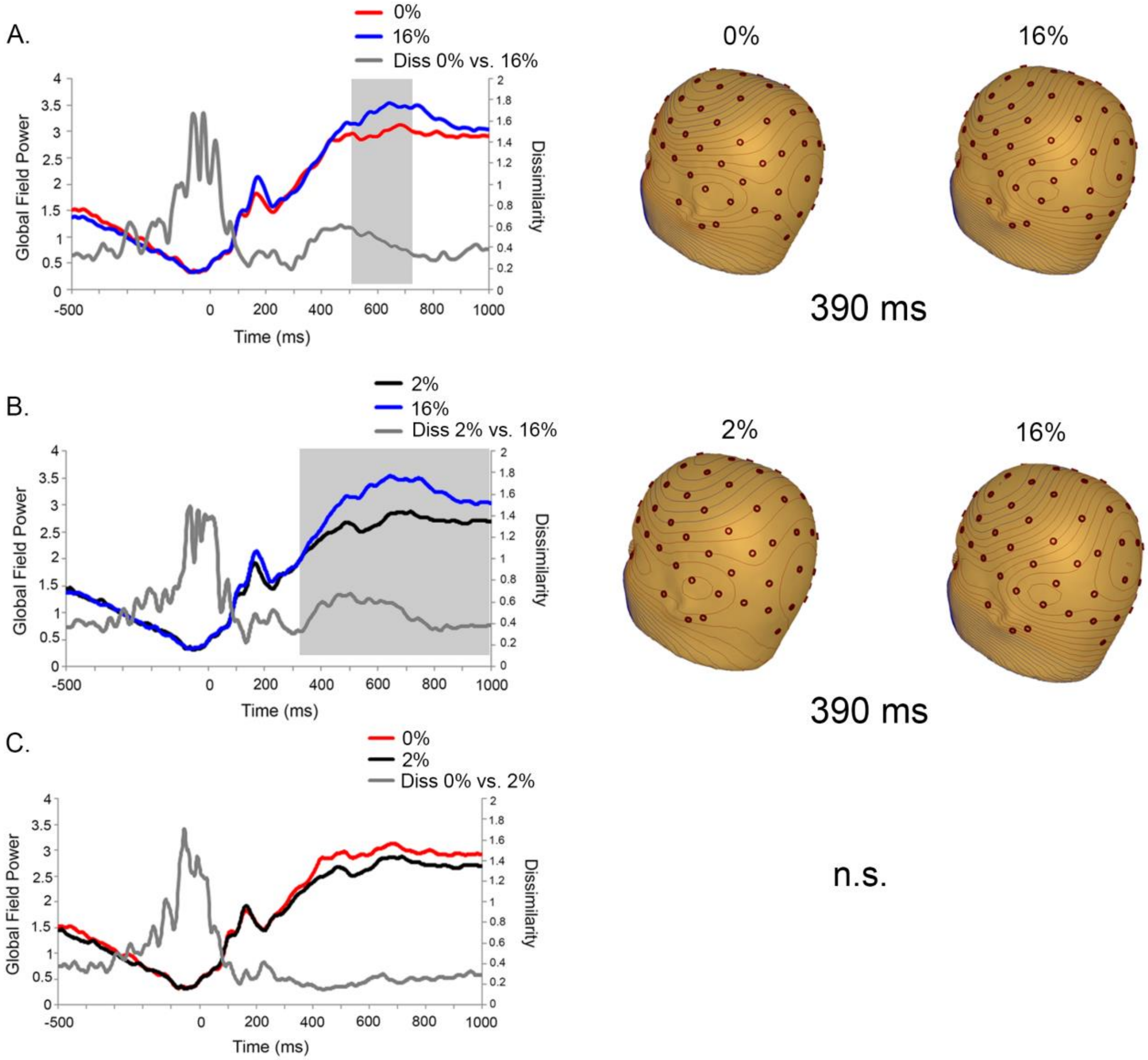

Figure 9. GFP and GMD plotted for each condition comparison during the context. Grey boxes indicate significant GMD time ranges. (A) Significant GMD time range for the 0% vs. 16% comparison was 300 ms – 720 ms. Corresponding topographies during the P400 time range (390 ms) are shown to the right. (B) Significant GMD time range for the 2% vs. 16% comparison was 311 ms – 1000 ms. Corresponding topographies during the P400 time range (390 ms) are shown to the right. No significant GMD was found for the 0% vs. 2% comparison.

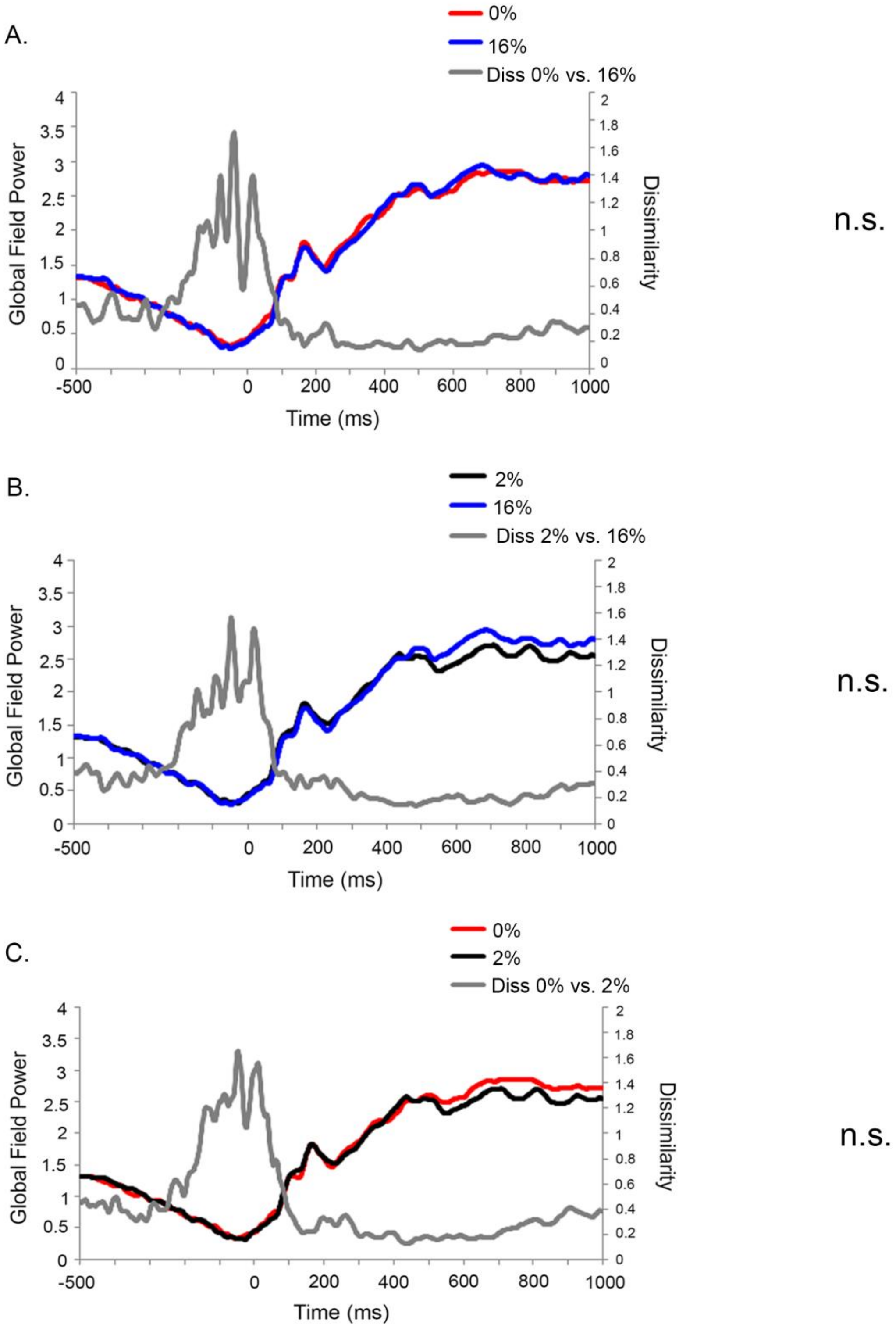

Figure 10. GFP and GMD plotted for each condition comparison during the test. (A) results for the 0% vs. 16% comparison. (B) results for the 2% vs. 16% comparison (C) results for the 0% vs. 2% comparison. All comparisons yielded non-significant results.

# CHAPTER 5

# DISCUSSION

## General Discussion

The current study has satisfactorily replicated several previous findings related to concurrent sound segregation while providing additional evidence with the use of two non-standard electrophysiological analyses. Behavioral data from the current study replicated the well-known effect of current mistuning such that greater mistuning percentages resulted in greater amounts of two object percepts (Moore et al., 1986; Hartmann et al., 1990; Alain et al., 2001; Alain et al., 2002; Alain & Izenberg, 2003; Alain, 2007; Arnott et al., 2011). Electrophysiological data replicated the presence of two components related to concurrent sound segregation: the ORN and P400. The ORN and P400 components were present during the context and increased in amplitude with greater mistuning percentages (Alain et al. 2001, Alain et al., 2002; Alain et al., 2003, Alain & Izenberg, 2003).

Additional non-traditional electrophysiological analyses were used to measure overall strength of neural activity (GFP) and overall topographical differences (GMD). This was a novel approach to analyzing the ORN and P400 components. There was a significant effect of GFP during the ORN time range signifying greater overall neural strength when the context stimulus was mistuned by 16% relative to the 0 and 2% conditions (Alain & Izenberg, 2003; Arnott et al., 2011). Fishman (2010) recorded neural activity within primary auditory cortex of monkeys using harmonic complex tones. They found increased activity in neuronal populations that were selectively tuned to the frequency of the mistuned harmonic. Their activity increased with greater mistuning percentages. The greater GFP found during the 16% condition likely reflects this process. The increased activity within primary auditory cortex to mistuned harmonic complex tones could increase the overall synchronization of neural activity and be reflected in the cortical recordings of the current study. However, there was no significant difference in GFP during the ORN time range between the 0% and 2% conditions. This could be due to the difference in frequency of the second harmonic between the 0% and 2% mistunings being too small (4 Hz) to elicit a significant result, especially when recording electrical activity from the scalp. While tonotopic areas of primary auditory cortex have been shown to be sensitive to small changes in frequency, a mistuning percentage that elicited significant differences in amplitude or response strength was 8% (Fishman, 2010). Results from the GMD analyses indicated no difference in scalp topographies between the 0, 2 and 16% conditions during the time range of the ORN. Previous research has shown the ORN has neural generators within primary auditory cortex (Alain & Izenberg, 2003). The absence of topographic differences in combination with the GFP results supports the notion that local neuronal populations selectively tuned to the frequency of the mistuned harmonic are increased in tonotopic areas of the auditory cortex when segregating concurrent objects. Finally, there was no effect of GFP during the time range of the P400 during the context; however, there were topographic differences between the 16% and 0% conditions as well as the 16% and 2% conditions. There were no topographic differences between the 0% and 2% conditions. The P400 is thought to reflect perceptual processes involved in making active judgments about whether there are one or two objects present (Alain et al., 2001; Alain et al. 2002). Behaviorally, the 0% and 2% conditions elicited a greater number of one object percepts when compared to the 16% condition. It is possible this result reflects the recruitment of additional brain areas when reporting a percept of two objects. For example, Cusack (2005) found activity within the intraparietal sulcus in addition to auditory cortex when participants perceived a sequence of alternating tones as two objects. Lastly, one of the aims of the current study was to investigate whether facilitative and contrastive context effects were present within a concurrent sound segregation task using harmonic complex tones. Behavioral results showed a significant effect of prior perception (facilitative) but no significant effect of prior mistuning (contrastive). Although not statistically significant, mistuning percentages presented during the context elicited smaller amplitudes during the ORN time range of the test ($p$ = .058) indicative of some form of adaptation.

The facilitative and contrastive effects explored in this study are well documented across several modalities; (Carter, Konkle, Wang, Hayward, & Moore, 2008; Carter, Snyder, Fung, & Rubin, 2014; Chopin & Mamassian, 2012; Riskey, Parducci, & Beauchamp, 1979; Hulshoff Pol, Hijman, Baare, & van Ree, 1998; Thiel et al., 2014; Huang & Holt, 2012; Kanai & Verstraten, 2005; Snyder, Carter, Lee, Hannon, & Alain, 2008; Pastukhov & Braun, 2013; Herr et al., 1982). However, the current study failed to find a significant effect of prior mistuning both behaviorally and electrophysiologically. A possible explanation for this could be the nature of the stimulus parameters; more specifically, the mistuning percentage used as the ambiguous stimulus, the duration of the context stimulus and the duration of the inter-stimulus interval.

The behavioral responses to the 2% mistuning suggest that this particular percentage was not truly ambiguous. As mentioned previously, there were an uneven amount of responses between the one object and two object percepts. When looking strictly at the 2% context responses, the total percentage of one object percepts was 34%. If the stimulus was truly ambiguous we would expect to see a total percentage of one object percepts around 50%. Overall, the 2% mistuning was typically perceived as one object and did not elicit true ambiguity. This follows the results of Moore et al. (1986) which indicated that the mistuned harmonic will pop out as a second object around 3% mistuning. Additionally, complex tones have been found to become ambiguous around 4% mistuning (Alain et al., 2001). If this is the case, the strong bias of perception being predominantly heard as either one or two objects (depending on the subject) could have overridden any perceptual effects arising from neural adaptation.

The favored explanation within the current literature is that contrastive effects are caused by adaptation or neural fatigue taking place during the presentation of the context stimulus. When presented with a subsequent ambiguous stimulus the activity of the neurons selectively tuned to the previous interpretation of the prior stimulus are weakened and the neurons selectively tuned to the opposite percept are now dominant (Toppino & Long, 2015; Long, Toppino & Mondin, 1992; Long & Moran, 2007; Snyder et al., 2008; Snyder et al., 2009; Kanai & Verstraten, 2005; Kohn & Movshon, 2004; Huk et al., 2001). However, context stimuli used in past studies are either sequences of repeating stimuli or stimuli of longer durations relative to the 400 ms context stimulus used in the current study. Additionally, shorter blank durations are used between the context and test, especially if short context durations are used. It could be that the relatively short duration of the context stimulus prevented adaptation from occurring, at least when relying on neural activity recorded from the scalp (i.e., EEG) and subjective perceptual measures. It could also be the case that some adaptation is occurring but because the interval between the context and test is 2000 ms, this results in recovery of adaptation. For example, Long and Moran (2007) were investigating the contrastive effect using the Necker Cube. They presented an unambiguous stimulus followed by an ambiguous stimulus and manipulated the timing of the blank duration (1 s, 10 s, or 100 s). They found that a contrastive effect was present for the 1 s condition but was completely abolished for the 10 s and 100 s conditions. This presumably allowed the neurons to recover from adaptation. Finally, the context stimulus used in the current study was not a repeating sequence which could have also potentially resulted in the absence of a contrastive effect. It has been shown that repeated presentations of brief adapters induce stronger contrastive effects than continuous context stimuli of the same total duration (Magnussen & Greenle, 1986). It is clear that the processes of adaptation are extremely sensitive to physical stimulus parameters and perhaps the ones used currently do not result in a perceptual contrastive effect. Theoretically, would it be beneficial for the auditory system to adapt under these circumstances?

Although the exact purposes of adaptation are still a mystery, there are several ideas that have been proven to be substantial. One idea is that adaptation protects against overstimulation within the sensory system. It is metabolically expensive for neurons to respond and therefore firing to a repeated stimulus is not advantageous to the sensory system (Megela & Teyler, 1975). Another functional purpose might be that it plays a role in the detection of changes and novelty within the environment. Evidence for this is provided by stimulus-specific adaptation and studies using an oddball paradigm which elicit an MMN response which is a deviant detection ERP component (Escera et al., 1998; Naatanen et al., 2005; Clifford et al., 2000). Stimulus-specific adaptation occurs when neuronal responses to a repeating stimulus decreases with repetition (Ulanovsky et al., 2003; Malmierca et al., 2009). The nature of the short stimulus durations used, the long blank intervals, and the use of multiple different stimulus pairs might not have required the sensory system to protect itself from overstimulation or to prepare itself for the detection of changes and novel stimuli. The current study did not use sequences of repeating stimuli with short blank intervals and there was no established standard and deviant stimulus. In line with these explanations of the functional purpose of adaptation, it seems to not be advantageous for the sensory system to adapt given these parameters. An additional purpose is to support efficient coding of environmental stimuli (Wark et al., 2007). Neurons have a limited capacity when it comes to responding to the wide range of environmental stimuli and it is beneficial for their response properties to change according to the stimulus variations within the environment to successfully extract the most information. Additionally, it has been argued that sensory systems can decide on an adaptation timescale that matches the changes in stimulus presentation in order to optimize their coding of incoming information (Wark et al., 2007). However, this type of efficient coding process occurs only when the time-scale of adaptation with the neurons involved is longer than the time scale of the changing stimulus parameters (Schwabe & Obermayer, 2002). The time scale that it takes for the neurons to adapt to the context stimulus and recover from the adaptation are not long enough to exceed the 400ms context duration or the 2000ms blank interval duration.

With this specific paradigm and stimulus parameters there was no effect of prior mistuning; however, there was an effect of prior perception. These pattern of results might exist because the facilitative effect does not appear to require long context stimulus durations and can also survive long blank intervals (Huber & O'riley, 2003; Nawrot & Blake, 1989; Kanai & Verstraten, 2005; Long, Toppino, & Mondin, 1992; Brascamp, 2007; Leopold, 2002; Pastkuhov &Braun, 2013). For example, in a study looking at the two types of context effects, the facilitative effect dominated until the context stimulus exceeded 500ms and then the effect reversed to be contrastive when using blank intervals of 71-412ms (Brascamp, 2007). Pastkuhov & Braun (2013) used a moving sphere that could be rotating either left or right to induce a contrastive and facilitative effect. They manipulated the context duration and the duration of the blank interval between the context and test. Results showed a contrastive effect when using a 1000ms context stimulus that was abolished when using a blank interval of 700ms. When ambiguous spheres with durations as little as 100ms were presented sequentially there was a priming effect that persisted for blank intervals of up to one minute.

While it is not the always the case that contrastive effects require long context durations with short blank intervals and facilitative effects require short stimulus durations with long blank intervals there is definitely a clear distinction between the temporal dynamics associated with each effect. These clear differences in temporal dynamics have led to conclusions that these effects arise from separate processes. Within the vision literature, both effects were studied using the motion after-effect. By presenting ambiguous and unambiguous directions of motion the facilitative and contrastive effect were induced, respectively. The contrastive effect was induced by a context stimulus of 320ms; however, it was greatly reduced with a blank interval of 1000ms and vanished with an ISI of 2000ms. The facilitative effect was also induced by the 320ms context duration but unlike the contrastive effect, was present even with blank intervals up to 5000ms (Kanai & Verstraten, 2005). The authors concluded that the contrastive effect occurs in earlier areas of the visual system such as primary visual cortex and perhaps even within the LGN where fast neural plasticity occurs (Nelson,1991; Stratford et al., 1996; Lisberger & Movshon,1999) and the facilitative effect is carried out mostly in later areas of the visual system such as area MT or V5 where slow gradual potentiation may occur.

The clear distinction in temporal dynamics is not the only empirical evidence researchers use to support the claim that two processes, or at least separate levels are involved, there is also support coming from functional brain imaging. A recent study used fMRI to investigate at what stages within the brain visual contrastive and facilitative effects occur and whether the processes are the same or different (Schwiedrzik et al., 2014). Behaviorally, they found no interaction between the two effects, suggesting separate processes. Furthermore, they found different cortical networks activated for each effect: contrastive effects were localized to lower visual areas while facilitative effects were localized to a wider range of areas such as higher-order visual and fronto-parietal areas.

These two-process theories have not gone unchallenged. Competing theories claim these effects can be explained as arising from one single process (Noest, 2007; Lages & Treisman, 2010). One explains that adaptation has two distinct effects: suppressive and enhancive. The suppressive effect is described as a reduction in response gain after the presentation of a context stimulus. The enhancive effect arises from an increase in baseline responses from the neurons associated with a certain percept which gives it a ‘head start’ once the stimulus reappears (Noest, 2007). The deciding factor of which perceptual effect will occur is the duration of the blank interval between successive stimuli. However, this proposed neural model is based on psychophysical data that used 2 minute sequences of flashing ambiguous stimuli and was characterizing the nature of perceptual reversals. Not using any unambiguous stimuli and the different timing parameters might prove difficult to make direct comparisons between the current study and this model. The two experiments carried out by Chopin and Mamassian (2012) that concluded these effects arise from a single process, termed predictive adaptation, took into account a longer stimulus history while the current study aimed to look at the effects of immediate context. Likewise, the fundamental difference of characterizing the effects using a long stimulus history could also complicate comparisons.

While theories explaining these effects arise from the same process do possess empirical support, they do not explain several results found within the literature. This includes the result that the facilitative effect continues to exist even when the test stimulus moves to a different retinotopic location from the context (Knapen et al., 2009) whereas the contrastive effect is abolished if this occurs (Knapen et al., 2010). In addition, contrastive effects only occur for test stimuli that are very similar to the context, while attractive effects allow for more variability between context and test (Gepshtein and Kubovy, 2005). These results exemplify the involvement of higher brain areas that possess neurons with broader tuning. Also, neurons in higher brain areas are shown to integrate and persist activity over longer time periods (Honey et al., 2012; Chaudhuri et al., 2015) coinciding with the results that the facilitative effect displays a longer time constant than the contrastive effect (Pastukhov and Braun, 2013). Other controversial results include the results from some neuroimaging studies looking at facilitative effects showing activation of pre-frontal and parietal regions (Schwierdzik, 2014; Sterzer & Rees, 2008), while some studies exploring the contrastive effect show activation within sensory areas (Huk et al., 2001).

I believe it is important to address the fundamental differences that exist between the two effects. These effects produce phenomenologically different perceptions and are typically induced by different types of stimulus parameters. The facilitative effect is typically induced by the sequential presentation of *ambiguous* stimuli (with a few exceptions: Brascamp et al., 2007; Kanai & Verstraten, 2005; Long & Moran, 2007; Wilton, 1985) whereas the contrastive effect is typically elicited by the presentation of an *unambiguous* stimulus followed by an ambiguous stimulus (with the exception of inevitable bi- and multi-stable switching). Facilitation effects are presumably driven by endogenous activity since the physical stimulus itself does not change whereas contrastive effects are driven by exogenous changes between the context and test. It is possible these different types of stimulus situations require different types of processing, at least at some level or in some manner. Ambiguous sensory processing may require a more refined perceptual decision making process because the stimulus itself is not providing the sensory system with sufficient information to make an efficient decision. For instance, parietal and prefrontal brain areas have been shown to be activated during the processing of ambiguous stimuli (Lumer & Rees, 1999; Lumer et al., 1998; Tomohiro, 2013). The recruitment of other brain areas, or additional levels of processing could be advantageous for stabilizing perceptions of ambiguous, incomplete, or disrupted stimuli.

It is difficult to draw compelling conclusions about whether these effects arise from the same or different processes from the current results. I was not able to analyze the electrophysiological data associated with the facilitative effect and some claims are being made based on negative data (i.e., the lack of prior mistuning effect). Nonetheless, I believe the current results along with results from previous literature can conclude that the presumed adaptation that leads to the contrastive effect is different than the specific process that leads to the facilitative effect. The current study utilized a paradigm that included a relatively short context duration (400 ms) with a relatively long blank interval between the context and test (2000 ms). These timing parameters resulted in the presence of a facilitative effect and no contrastive effect suggesting the two effects emerge from different temporal dynamics. Indeed, previous literature manipulating timing variables have consistently shown support for this interpretation (Kanai & Verstraten, 2005; Brascamp, 2007; Pastkuhov & Braun, 2013). The contrastive effect seems to involve neurons within lower-levels that are more sensitive to stimulus features and timing information whereas neurons involved in the facilitative effect are less sensitive to featural changes and can persist activation over longer time constants. Although the current study is not able to compare ERP’s for the facilitative effect the behavioral data indicates that there is a sustained process going on that persists for several seconds, unlike the effect of prior mistuning. This result is in line with Snyder et al. (2009) which showed positive sustained ERPs during the test that began at the start of the stimulus presentation. Conversely, the effect of prior mistuning did not start at the beginning of the test and the modulations were transient. This study was specifically studying auditory context effects using a sequential stream segregation paradigm that is used to investigate auditory scene analysis.

The stimuli used in the current study are often used to investigate auditory scene analysis; more specifically, concurrent sound segregation (Alain & Izenberg, 2003; Arnott et al., 2011, Alain, 2001; Alain & Dyson, 2008). Past studies looking at concurrent sound segregation have posited that the ORN component is an index of automatic concurrent sound segregation given that it is present even without focused attention. It is not known whether the modulations of the ORN occur due to the physical manipulations of the stimulus or if they also occur because of perceptual processes. Given there was a trend of adaptation within the ORN time range during the test without the accompanying behavioral effect could be interpreted as the ORN being an automatic process that does not represent perception but more likely represents stimulus properties. The results from the current study revealed that the auditory system is not only using the current available sensory information but also relies on previous perceptions and physical stimuli to make perceptual decisions. The exact processes that occur when organizing our auditory environments are still a mystery. However, it is clear that the processes responsible are complex, involving multiple levels with neurons that are sensitive to stimulus history and temporal dynamics.

There remains much to be learned about the processes that result in the two context effects and how they are affected by factors such as extent of stimulus history, timing parameters, and the amount of available stimulus information (i.e., ambiguous vs. unambiguous stimuli).  Future studies using methods such as fMRI, ECoG (electrocorticography), MEG (magnetoencephalography) and transcranial magnetic stimulation (TMS) can further elucidate whether there are additional or different brain areas associated with the two effects. Using identical stimulus paradigms during these different techniques would be advantageous to assist in making confident comparisons and integrations between the findings. The spatial resolution of fMRI, invasive nature of ECoG, temporal resolution of MEG and “lesion” effects of TMS would provide valuable insight into the brain areas involved and their temporal sequences. Additionally, animal studies that record directly from single or groups of neurons within different levels of auditory cortex can help to characterize adaptation effects that might play a role in context effects. In attempts to elicit a contrastive effect using harmonic complex tones and characterize the dynamics of each effect future behavioral studies can alter stimulus parameters. For example, varying the context duration, the inter-stimulus interval and the inter-trial interval will reveal the temporal dynamics of each effect and how they are impacted by these changes. The current study revealed the inter-subject variability that exists in regards to stimulus ambiguity. Future studies would benefit from using an adaptive procedure in which stimulus ambiguity is determined for each subject prior to testing. While this study focused on investigating the effects of immediate context, it would also be beneficial for future studies to use longer stimulus contexts to determine the effects of stimulus history.

## Conclusions

One of the aims of the current study were to assess whether two different context effects are present during a concurrent sound segregation task. Results showed the presence of a facilitative effect but no presence of a contrastive effect. It seems likely that these results occurred because of specific stimulus parameters, showing the sensitivity that the contrastive effect is susceptible to. A second aim was to find evidence relating to the levels of processing at which these effects occur. Unfortunately, I was not able to analyze the EEG data relating to the facilitative effect and there were no statistically significant modulations relating to the contrastive effect. This along with the absence of a behavioral contrastive effect limited my ability to draw compelling conclusions relating to levels of processing and determining whether two separate processes or one single process are responsible for producing the effects. Nevertheless, I believe the nature of the current results along with previous literature provide support for a process that originates in sensory areas for both effects but then additional processing is needed for the facilitative effect. The less sensitive nature and the greater ability to persist over longer time intervals during the facilitative effect suggests processing that occurs within higher levels. Another possibility could be that the facilitative effect recruits and is more responsive to feedback connections from higher brain regions such as frontal and parietal areas. Further research utilizing brain imaging and physiological techniques along with altering timing parameters will serve to provide additional information needed to characterize and understand aspects of sensory processing from all modalities.

# APPENDIX I: DEMOGRAPHIC QUESTIONNAIRE

**Participant Code: ___________________**

***Screening Questions***

***Please answer the following questions completely and honestly.***

***All of your responses will remain confidential.***

1. Birth Date ________/______/________
   Month Day Year
2. Age? _________
3. What is the first language you learned? _____________________
4. If English is not your first language, at what age did you begin learning English? _____________
5. Gender **Male** **Female**
6. Are you left handed, right handed, or ambidextrous? **Left** **Right** **Ambidextrous**
7. Is your vision corrected (glasses/contacts)? **Yes** **No**
   Are you wearing them now? **Yes** **No**
8. Do you have severe visual impairments, such as cataracts or glaucoma? **Yes** **No**
9. Do you have any hearing loss (hearing aid)? **Yes** **No**
10. Do you have experience learning or playing music (including singing)? **Yes** **No**
    If **Yes**, list instruments, number of years for each, and number of years in formal training for each:
    ________________________________________________________________
    ________________________________________________________________
    ________________________________________________________________
11. Have you ever had a head injury (e.g., automobile accident, fall, sports injury)? **Yes** **No**
12. Have you ever or do you now have seizures? **Yes** **No**
13. Have you ever been unconscious? **Yes** **No** If so, for how long? _________________
14. Do you have any neurological disorders? **Yes** **No** (*please describe*) _______________________
    ________________________________________________________________
    ________________________________________________________________
15. Have you ever had any kind of brain surgery? **Yes** **No** If yes, type: __________________________

16. Do you have any medical conditions (including substance abuse)? **Yes** **No** (*please describe*) ___

_______________________________________________

_______________________________________________

17. Have you been diagnosed with any mental or psychiatric disorder? **Yes** **No** (*please describe*) ___

_______________________________________________

_______________________________________________

# APPENDIX II: IRB APPROVAL

**UNLV Social/Behavioral IRB - Expedited Review**
**Continuing Review Approved**

| | |
|---|---|
| **DATE:** | November 2, 2016 |
| **TO:** | Joel Snyder |
| **FROM:** | UNLV Social/Behavioral IRB |
| **PROTOCOL TITLE:** | [710883-20] Neural Mechanisms of Auditory and Visual Processing in Healthy Adults |
| **SUBMISSION TYPE:** | Continuing Review/Progress Report |
| **ACTION:** | APPROVED |
| **APPROVAL DATE:** | November 2, 2016 |
| **EXPIRATION DATE:** | November 1, 2017 |
| **REVIEW TYPE:** | Expedited Review |

Thank you for submission of Continuing Review/Progress Report materials for this protocol. The UNLV Social/Behavioral IRB has APPROVED your submission. This approval is based on an appropriate risk/benefit ratio and a protocol design wherein the risks have been minimized. All research must be conducted in accordance with this approved submission.

This IRB action will reset your expiration date for this protocol. The protocol is approved for a period of one year from the date of IRB approval. The new expiration date for this protocol is November 1, 2017.

**PLEASE NOTE:**
Attached with this approval notice is the **official Informed Consent/Assent (IC/A) Form** for this study. Only copies of this official IC/A form may be used when obtaining consent. Please keep the original for your records.

Should there be *any* change to the protocol, it will be necessary to submit a **Modification Form** through ORI - Human Subjects. No changes may be made to the existing protocol until modifications have been approved.

ALL UNANTICIPATED PROBLEMS involving risk to subjects or others and SERIOUS and UNEXPECTED adverse events must be reported promptly to this office. Please use the appropriate reporting forms for this procedure. All FDA and sponsor reporting requirements should also be followed.

All NONCOMPLIANCE issues or COMPLAINTS regarding this protocol must be reported promptly to this office.

This protocol has been determined to be a Minimal Risk protocol. Based on the risks, this protocol requires continuing review by this committee on an annual basis. Submission of the **Continuing Review Request Form** must be received with sufficient time for review and continued approval before the expiration date of November 1, 2017.

If you have questions, please contact the Office of Research Integrity - Human Subjects at IRB@unlv.edu or call 702-895-2794.

# REFERENCES

Addams, R. (1834). An account of a peculiar optical phenomenon seen after having looked at a moving body. *London and Edinburgh Philosophical Magazine and Journal of Science, 5*, 373-374.

Alain, C. (2007). Breaking the wave: effects of attention and learning on concurrent sound perception. *Hearing Research,229*, 225-236. doi: 10.1016/j.heares.2007.01.011

Alain, C., Arnott, S. R., & Picton, T. W. (2001). Bottom-up and top-down influences on auditory scene analysis: Evidence from event-related brain potentials. *Journal of Experimental Psychology: Human Perception and Performance, 27*(5), 1072-1089.

Alain, C., Dyson, B. J., & Snyder, J. S. (2006). Aging and the perceptual organization of sounds: A change of scene? In P. M. Conn (Ed.), *Handbook of models for human aging,* (759-770). New York: Elsevier Academic Press.

Alain, C., & Izenberg, A. (2003). Effects of attentional load on auditory scene analysis. *Journal of Cognitive Neuroscience, 15*(7), 1063-1073. doi: 10.1162/089892903770007443

Alain, C., Schuler, B.M., & McDonald, K.L. (2002). Neural activity associated with distinguishing concurrent auditory objects. *Journal of the Acoustical Society of America, 111*, 990-995. doi: 10.1121/1.1434942

Alain, C., Theunissen, E.L., Chevalier, H., Batty, M., & Taylor, M.J. (2003). Developmental changes in distinguishing concurrent auditory objects. *Cognitive Brain Research, 16*, 210-218. doi:10.1016/S0926-6410(02)00275-6

Albright, T.D. (1993). Cortical processing of visual motion. In Visual Motion and Its Role in the Stabilization of Gaze, F.A. Miles and J. Wallman, eds. (New York: Elsevier), pp.177-201.

Alcantara, J. I., Weisblatt, E. J., Moore, B. C., & Bolton, P. F. (2004). Speech-in-noise perception in high-functioning individuals with autism or Asperger's syndrome. *Journal of Child Psychology and Psychiatry, 45*(6), 1107-1114. doi: 10.1111/j.1469-7610.2004.t01-1-00303.x

Arnott, S.R., Bardouille, T., Bernhard, R., & Alain, C. (2011). Neural Generators underlying concurrent sound segregation. *Brain Research,1387*, 116-124. doi:10.1016/j.brainres.2011.02.062

Bidet-Caulet, A., Fischer, C., Bauchet, F., Aguera, P.E., & Bertrand, O. (2007). Neural substrate of concurrent sound perception: direct electrophysiological recordings from human auditory cortex. *Frontiers in Human Neuroscience,1*, 5. doi: 10.3389/neuro.09.005.2007

Bregman, A. S. (1990). *Auditory scene analysis: The perceptual organization of sound*. Cambridge, MA: MIT Press.

Carter, O., Konkle, T., Wang, Q., Hayward, V., & Moore, C. (2008). Tactile rivalry demonstrated with an ambiguous apparent-motion quartet. *Current Biology, 18*(14), 1050-1054. doi: 10.1016/j.cub.2008.06.027

Carter, O., Snyder, J.S., Fung, S., and Rubin, N. (2014). Using ambiguous plaid stimuli to investigate the influence of immediate prior experience on perception. *Attention, Perception and Psychophysics, 76*, 133-147. doi: 10.3758/s13414-013-0547-5

Chaudhuri, R.,Knoblauch,K.,Gariel,M.A.,Kennedy,H.,andWang,X.J. (2015). Alarge-scalecircuitmechanismforhierarchicaldynamicalprocessing in theprimatecortex. *Neuron* 88, 419–431.doi:10.1016/j.neuron.2015. 09.008

Chen, X., and He, S. (2004). Local factors determine the stabilization of monocular ambiguous and binocular rivalry stimuli. *Current Biology, 14*, 1013-1017.

Chopin, A., & Mamassian, P. (2012). Predictive properties of visual adaptation. *Current Biology, 22*, 622-626. doi: 10.1016/j.cub.2012.02.021

Clifford, C.W.,Wenderoth,P., & Spehar,B.(2000).A functional angle on some after-effects in cortical vision. *Proc. Biol. Sci.* 267, 1705–1710.doi:10.1098/rspb. 2000.1198

Cuffin, B.N. (1998, Sept.-Oct.). EEG dipole source localization. *Engineering in Medicine and Biology Magazine, IEEE, 17*(5), 118-122.
doi: 10.1109/51.715495

Cusack, R. (2005). The intraparietal sulcus and perceptual organization. *Journal of Cognitive Neuroscience, 17*(4), 641-651.

Dyson, B., Alain, C., & He, Y. (2005). Effects of visual attentional load on low-level auditory scene analysis. *Cognitive, Affective, and Behavioral Neuroscience,5*, 319-338. doi: 10.3758/CABN.5.3.319

Gibson, J. J., & Radner, M. (1937). Adaptation, after-effect and contrast in the perception of tilted lines. I. Quantitative studies. *Journal of Experimental Psychology, 20*, 453-467.

Herr, P.M., Sherman, S.J. & Fazio, R.H. (1983). On the consequences of priming: Assimilation and contrast effects. *Journal of Experimental Social Psychology, 19*, 323-340.

Hartmann, W.M., McAdams, S., & Smith, B.K. (1990). Hearing a mistuned harmonic in an otherwise periodic complex tone. *Journal of Acoustical Society of America, 88*, 1712-1724.

Honey, C.J.,Thesen,T.,Donner,T.H.,Silbert,L.J.,Carlson,C.E.,Devinsky., O., et al.(2012).Slow cortical dynamics and the accumulation of information over long timescales. *Neuron* 76, 423–434.doi:10.1016/j.neuron.2012. 08.011

Huang, J., & Holt, L. L. (2012). Listening for the norm: adaptive coding in speech categorization. *Frontiers in Psychology, 3*, 10. doi: 10.3389/fpsyg.2012.00010

Huber, D. E., & O'Reilly, R. C. (2003). Persistence and accommodation in short-term priming and other perceptual paradigms: Temporal segregation through synaptic depression. Cognitive Science, 27, 403–430.

Huk, A. C., Ress, D., & Heeger, D. J. (2001). Neuronal basis of the motion aftereffect reconsidered. *Neuron, 32*(1), 161-172. doi: S0896-6273(01)00452-4 [pii]

Hulshoff Pol, H. E., Hijman, R., Baare, W. F., & van Ree, J. M. (1998). Effects of context on judgements of odor intensities in humans. *Chemical Senses, 23*(2), 131-135.

Kanai, R., & Verstraten, F. A. (2005). Perceptual manifestations of fast neural plasticity: motion priming, rapid motion aftereffect and perceptual sensitization. *Vision Research, 45*(25-26), 3109-3116. doi: 10.1016/j.visres.2005.05.014

Kohn, A. & Movshon, A.J. (2004). Adapatation changes the direction tuning of macaque MT neurons. *Nature Neuroscience, 7*(7), 764-772. doi: 10.1038/nn1267

Lages, M., & Treisman, M. (2010). A criterion setting theory of discrimination learning that accounts for anisotropies and context effects. *Seeing and Perceiving, 23*, 401-434. doi: 10.1163/187847510X541117

Lisberger, S., &Movshon, J. (1999). Visual motion analysis for pursuit eye movements in area MT of macaque monkeys. Journal of Neuroscience, 19, 2224–2246.

Leopold, D.A., Wilke, M., Maier, A., & Logothetis, N.K. (2002). Stable perception of visually ambiguous patterns. *Nature Neuroscience, 6*, 605-609.

Long, G. M., Toppino, T. C., & Mondin, G. W. (1992). Prime time: Fatigue and set effects in the perception of reversible figures. *Perception & Psychophysics, 52*, 609–616.

Long, G.M.,&Moran, C. J. (2007). How to keep a reversible figure from reversing: Teasing out top-down and bottom-up processes. *Perception*, *36*, 431–445.

Luck, S. J. (2005). An Introduction to the Event-Related Potential Technique. Cambridge, MA: MIT Press.

Luck, S. J. (2012). "Event-related potentials," in APA Handbook of Research Methods in Psychology: Vol. 1, Foundations, Planning, Measures, and Psychometrics, eds H. Cooper, P. M. Camic, D. L. Long, A. T. Panter, D. Rindskopf, and K. J. Sher (Washington, DC:American Psychological Association), 523–546

Lumer, E. D., Friston, K. J., & Rees, G. (1998). Neural correlates of perceptual rivalry in the human brain. Science, 280, 1930–1934.

Lumer, E. D., & Rees, G. (1999). Covariation of activity in visual and prefrontal cortex associated with subjective visual perception. Proceedings of the National Academy of Science USA, 96, 1669–1673.

Magnussen, S. & Greenlee, M.W. (1986). Temporal aspects of spatial adaptation. A study of the tilt aftereffect. Vision Research 26, 661-672.

Maier, A., Wilke, M., Logothetis, N.K., and Leopold, D.A. (2003). Perception of temporally interleaved ambiguous patterns. *Current Biology, 13*, 1076-1085.

Megela,A.L.,andTeyler,T.J.(1979).Habituation and the human evoked potential. *J. Comp.Physiol.Psychol.* 93, 1154–1170.doi:10.1037/h0077630

Moore, B.C., Glasberg, B.R., & Peters, R.W. (1986). Thresholds for hearing mistuned partials as separate tones in harmonic complexes. *Journal of the Acoustical Society of America, 80*, 479-483.

Nawrot, M., & Blake, R. (1989). Neural integration of information specifying structure from stereopsis and motion. *Science*, *244*, 716–718.

Nelson, S. B. (1991). Temporal interactions in the cat visual system. *Journal of Neuroscience, 11,* 344–356.

Noest, A. J., van Ee, R., Nijs, M. M., & van Wezel, R. J. (2007). Percept-choice sequences driven by interrupted ambiguous stimuli: A low-level neural model. *Journal of Vision, 7*(8), 10. doi: 10.1167/7.8.10/7/8/10/

Oruc, I., & Barton, J. J. (2010). A novel face aftereffect based on recognition contrast thresholds. *Vision Research, 50*(18), 1845-1854. doi: 10.1016/j.visres.2010.06.005

Pashler, H., and Wagenmakers, E. J. (2012). Editors' introduction to the special section on replicability in psychological science: a crisis of confidence? Perspect. *Psychological Science, 7*, 528–530. doi: 10.1177/1745691612465253

Pastukhov, A. and Braun, J. (2013). Disparate time-course of adaptation and facilitation in multi-stable perception. *Learning and Perception, 5*, 101-118. doi: 10.1556/LP.5.2013.Suppl2.7

Pearson, J., and Clifford, C.W.G. (2004). Determinants of visual awareness following interruptions during rivalry. *Journal of Vision, 4*, 196-202.

Pearson, J., & Clifford, C.W.G. (2005). Mechanisms selectively engaged in rivalry: normal vision habituates, rivalrous vision primes. *Vision Research, 45,* 707-714.

Petkov, C. I., O'Connor K, N., Benmoshe, G., Baynes, K., & Sutter, M. L. (2005). Auditory perceptual grouping and attention in dyslexia. *Cognitive Brain Research, 24*(2), 343-354.

Riskey, D. R., Parducci, A., & Beauchamp, G. K. (1979). Effects of context in judgments of sweetness and pleasantness. *Perception & Psychophysics, 26*(3), 171-176. doi: 10.3758/Bf03199865

Sandberg, K., Barnes, G.R., Bahrami, B., Kanai, R., Overgaard, M. & Rees, G. (2014). Distinct MEG correlates of conscious experience, perceptual reversals and stabilization during binocular rivalry. *Neuroimage, 100*, 161-175.

Schwabe, L., & Obermayer, K. (2002). Rapid adaptation and efficient coding. *Biosystems, 67*(1-3), 239-244. doi: 10.1016/S0303-2647(02)00082-5

Schwiedrzik, C. M., Ruff, C. C., Lazar, A., Leitner, F. C., Singer, W., & Melloni, L. (2012). Untangling perceptual memory: Hysteresis and adaptation map into separate cortical networks. *Cerebral Cortex, 24*(5), 1152-64. doi: 10.1093/cercor/bhs396

Smith, A.T., Greenlee, M.W., Singh, K.D., Kraemer, F.M., and Hennig, J. (1998). The processing of first- and second-order motion in human visual cortex assessed by functional magnetic resonance imaging (fMRI). *Journal of Neuroscience, (18)*, 3816-3830.

Snyder, J. S., Carter, O. L., Lee, S.-K., Hannon, E. E., & Alain, C. (2008). Effects of context on auditory stream segregation. *Journal of Experimental Psychology: Human Perception and Performance, 34*, 1007-1016. doi: 10.1037/0096-1523.34.4.1007

Snyder, J. S., Carter, O. L., Hannon, E. E., & Alain, C. (2009a). Adaptation reveals multiple levels of representation in auditory stream segregation. *Journal of Experimental Psychology: Human Perception and Performance, 35*, 1232-1244. doi: 10.1037/a0012741

Snyder, J. S., Holder, W. T., Weintraub, D. M., Carter, O. L., & Alain, C. (2009b). Effects of prior stimulus and prior perception on neural correlates of auditory stream segregation. *Psychophysiology, 46*, 1208-1215. doi: 10.1111/j.1469-8986.2009.00870.x

Snyder, J. S., & Weintraub, D. M. (2011). Pattern specificity in the effect of prior $\Delta f$ on auditory stream segregation. *Journal of Experimental Psychology: Human Perception and Performance, 37*(5), 1649-1656. doi: 10.1037/a0023098

Snyder, J. S., & Weintraub, D. M. (2013). Loss and persistence of implicit memory for sound: Evidence from auditory stream segregation context effects. *Attention Perception & Psychophysics*. doi: 10.3758/s13414-013-0460-y

Sterzer, P., & Rees, G. (2008). A neural basis for percept stabilization in binocular rivalry. *Journal of Cognitive Neuroscience,* 20(3), 389-399. doi: 10.1162/jocn.2008.20039

Stratford, K. J., Tarczy-Hornuch, K., Martin, K. A. C., Bannister, N. J., & Jack, J. J. B. (1996). Excitatory synaptic inputs to spiny stellate cells in cat visual cortex. *Nature, 382*, 258–261.

Thiel, S. D., Bitzer, S., Nierhaus, T., Kalberlah, C., Preusser, S., Neumann, J., . . . Pleger, B. (2014). Hysteresis as an implicit prior in tactile spatial decision making. *PLoS ONE, 9*(2). doi: 10.1371/journal.pone.008980

Tomohiro, I. (2013). Disambiguation of ambiguous figures in the brain. *Frontiers in Human Neuroscience, 7*(501), 1-9. doi: 10.3389/fnhum.2013.00501

Tootell, R.B., Mendola, J.D., Hadjikhani, N.K., Ledden, P.J., Liu, A.K., Reppas, J.B., Sereno, M.I., & Dale, A.M. (1997). Functional analysis of V3A and related areas In human visual cortex. *Journal of Neuroscience. 17*, 7060-7078.

Toppino, T.C., & Long, G.M. (2015). Time for a change: what dominance durations reveal about adaptation effects in the perception of a bi-stable reversible figure. *Attention, Perception, and Psychophysics*, *77*(3), 867-882. doi: 10.3758/s13414-014-0809-x

Treisman, M. andWilliams, T.C. (1984). A theory of criterion setting with an application to sequential dependencies, *Psychological Review. 91*, 68–111. doi: 10.1037/0033-295X.91.1.68

Ulanovsky, N., Las, L., Farkas, D., & Nelken, I. (2004). Multiple time scales of adaptation in auditory cortex neurons. *Journal of Neuroscience, 24*(46), 10440-10453. doi: 10.1523/JNEUROSCI.1905-04.2004

Van Noorden, L. P. A. S. (1975). Temporal coherence in the perception of tone sequences. *Unpublished doctoral dissertation, Eindhoven University of Technology, Eindhoven*.

Vernet, M., Brem, A., Farzan, F., & Pascual-Leone, A. (2015) Synchronous and opposite roles of the parietal and prefrontal cortices in bistable perception: a double coil TMS-EEG study. *Cortex, 64*, 78-88. doi: 10.1016/j.cortex.2014.09.021

Wark, B., Lundstrom, N. B., Fairhall, A. (2007). Sensory adaptation. *Current Opinion in Neurobiology, 17*, 423-429. doi: 10.1016/j.conb.2007.07.001

Weintraub, D. M., Ramage, E. M., Sutton, G., Ringdahl, E., Boren, A., Pasinski, A. C., . . . Snyder, J. S. (2012). Auditory stream segregation impairments in schizophrenia. *Psychophysiology, 49*(10), 1372-1383. doi: 10.1111/J.1469-8986.2012.01457.X

Wilson, H. R. (2007). Minimal physiological conditions for binocular rivalry and rivalry memory. *Vision Research*, *47*(21), 2741-2750. doi: 10.1016/j.visres.2007.07.007

Wilton, R.N. (1985) The recency effect in the perception of ambiguous figures. *Perception*, 14, 53–61.

CURRICULUM VITAE

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## EDUCATION

2013-Present University of Nevada, Las Vegas
Experimental Psychology Ph.D Program
Anticipated completion: 2018
Advisor: Dr. Joel Snyder

2008-2012 University of Nevada, Las Vegas
Bachelor of Arts in Psychology

## PUBLICATIONS

Snyder, J.S., **Yerkes, B.D.,** Irsik, V.C., Vanden Bosch der Nederlanden, C. (In press). Varieties of attention affect auditory perception of scenes. *The Journal of the Acoustical Society of America.*

Snyder, J. S., **Yerkes, B. D.**, & Pitts, M., (2015). Testing domain-general theories of perceptual awareness with auditory brain responses. *Trends in Cognitive Science, 19*(6), 295-297.

Ramage, E., Klimas, N., Vogel, S., **Yerkes, B.D.,** Flores, A., Sutton, G…Snyder, J.S. (2015). Concurrent sound segregation impairments in schizophrenia: The contribution of auditory-specific and general cognitive factors. *Schizophrenia Research*.

## PROFESSIONAL PRESENTATIONS

**Yerkes, B. D.,** (2016, November). *Organizing sound: Influences of the past and present.* Talk given at the UNLV 3 Minute Thesis Competition in Las Vegas, Nevada – Semi-finalist.

**Yerkes, B. D.**, Weintraub, D., Snyder, J. S., (2016, June). *Stimulus-based attention and task-based attention modulate different auditory context effects.* Poster presented at the Association for the Scientific Study of Consciousness Research Conference in Buenos Aires, Argentina.

**Yerkes, B. D.,** (2016, March). *Assessing the influences of low- and high-level factors during auditory processing in individuals with autism.* Talk given to the UNLV Psychology

Department in Las
Vegas, Nevada.

**Yerkes, B. D.**, Weintraub, D., Snyder, J. S., (2016, February). *Auditory context effects during processing of mistuned harmonic tones: Behavioral and electrophysiological evidence.* Poster presented at the Association for Research in Otolaryngology Conference in San Diego, California.

**Yerkes, B. D.,** (2015, November). *Auditory processing in children with autism.* Talk given at the UNLV 3 Minute Thesis Competition in Las Vegas, Nevada – Semi-finalist.

**Yerkes, B. D.,** (2015, January). *Neural mechanisms underlying auditory context effects.* Talk given to the UNLV Psychology Department in Las Vegas, Nevada.

**Yerkes, B. D.,** (2014, November). *Neural mechanisms of auditory context effects.* Talk given at the UNLV 3 Minute Thesis Competition in Las Vegas, Nevada – Semi-finalist.

**Yerkes, B. D.,** (2014, February). *Attention modulates auditory stream segregation context effects.* Talk given to the UNLV Psychology Department in Las Vegas, Nevada.

**Yerkes, B. D.**, Weintraub, D., Snyder, J. S., (2013, July). *Attention modulates auditory stream segregation context effects.* Poster presented at the Association for the Scientific Study of Consciousness Research Conference in San Diego, California.

## HONORS AND AWARDS

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|---|---|
| 2016, August | University of Nevada, Las Vegas Graduate Access Grant<br>Amount awarded: $2,100 |
| 2016, August | University of Nevada, Las Vegas Summer Scholarship<br>Amount awarded: $2,000 |
| 2015, August | University of Nevada, Las Vegas Student Summer Faculty Research Grant<br>Amount awarded: $3,000 |
| 2015, August | University of Nevada, Las Vegas Graduate Access Grant<br>Amount awarded: $2,100 |

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|---|---|
| 2014, Summer | The Dynamics of Music and Language Summer School, University of California, Merced, Merced, CA. |