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The Effect of Prenatal Auditory Enrichment on Perceptual Narrowing in Bobwhite Quail Neonates

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

THE EFFECT OF PRENATAL AUDITORY ENRICHMENT ON PERCEPTUAL
NARROWING IN BOBWHITE QUAIL NEONATES

A dissertation submitted in partial fulfillment of

The requirements for the degree of

DOCTOR OF PHILOSOPHY

in

PSYCHOLOGY

by

Briana O'Dowd

2014

To: Interim Dean Michael R. Heithaus
College of Arts and Sciences

This dissertation, written by Briana O'Dowd, and entitled The Effect of Prenatal Auditory Enrichment on Perceptual Narrowing in Bobwhite Quail Neonates, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

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Date of Defense: October 10, 2014

The dissertation of Briana O'Dowd is approved.

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DEDICATION

I wish to dedicate this dissertation to my family, particularly my grandfather, David Alfred O'Dowd and, his brother, Denis La Pierre O'Dowd. Throughout their lives they served their country in World War II and their community teaching in inner-city Chicago public schools. Their character of devotion and humility has been something I aspire to and find solace within.

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ABSTRACT OF THE DISSERTATION

THE EFFECT OF PRENATAL AUDITORY ENRICHMENT ON PERCEPTUAL
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by

Briana O'Dowd

Florida International University, 2014

Miami, Florida

Professor Robert Lickliter, Major Professor

The development of species-typical perceptual preferences has been shown to depend on a variety of socially and ecologically derived sensory stimulation during both the pre- and postnatal periods. The prominent mechanism behind the development of these seemingly innate tendencies in young organisms has been hypothesized to be a domain-general pan-sensory selectivity process referred to as perceptual narrowing, whereby regularly experienced sensory stimuli are honed in upon, while simultaneously losing the ability to effectively discriminate between atypical or unfamiliar sensory stimulation. Previous work with precocial birds has been successful in preventing the development of species-typical perceptual preferences by denying the organism typical levels of social and/or self-produced stimulation. The current series of experiments explored the mechanism of perceptual narrowing to assess the malleability of a species-typical auditory preference in avian embryos. By providing a variety of different unimodal and bimodal presentations of a mixed-species vocalizations at the onset of prenatal auditory function, the following project aimed to 1) keep the perceptual window from narrowing, thereby interfering with the development of a species-typical auditory preference, 2) investigate how long

differential prenatal stimulation can keep the perceptual window open postnatally, 3) explore how prenatal auditory enrichment effected preferences for novelty, and 4) assess whether prenatal auditory perceptual narrowing is affected by modality specific or amodal stimulus properties during early development. Results indicated that prenatal auditory enrichment significantly interferes with the emergence of a species-typical auditory preference and increases openness to novelty, at least temporarily. After accruing postnatal experience in an environment rich with species-typical auditory and multisensory cues, the effect of prenatal auditory enrichment rapidly was found to rapidly fade. Prenatal auditory enrichment with extraneous non-synchronous light exposure was shown to both keep the perceptual narrowing window open and impede learning in the postnatal environment, following hatching. Results are discussed in light of the role experience plays in perceptual narrowing during the perinatal period.

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CHAPTER I

INTRODUCTION

The seemingly effortless and reliable emergence of species-typical perceptual preferences and behaviors has long been attributed to innate genetic predispositions. While proponents of nativism claim that species-specific tendencies observable at birth or hatch are the result of hard-wired genetic programs, they ignore the rich experiential history of embryonic development and prenatal stimulus exposure. A particular point of contention between nativists and developmental systems theorists has been the emergence of species-typical perceptual preferences, most notably of species-typical auditory stimuli. The process of differentiating, recognizing, and favoring a particular native class of auditory stimuli early in development has long been mislabeled as “imprinting” and attributed to genetic encoding.

The notion of behavioral and perceptual canalization the results from experience in a particular ontogenetic niche has been recognized by developmentalists since the early 1930s. The earliest account of behavioral canalization was that of stereotypical fetal motor patterns associated with the behavioral contingencies afforded by the in-utero environment (Holt, 1931). In the latter half of the century, Kuo (1967) transformed this strict behaviorist explanation of canalization due to reinforcement to include all the complexities of the developmental system, including, but not limited to developmental history, biological constraints, and passive environmental stimulation. Kuo’s (1967) elucidation of behavioral and perceptual canalization to include the bidirectional and longitudinal interactions between biological and environmental factors provided the underpinnings for Gottlieb’s ecological systems theory and modern developmental

systems theory. In this model, species-typical biological, ecological, and experiential consistency fosters the so-called “native” or familiar pattern of behavior and perceptual preference typically observed for that species. Early alterations to any part of the system can have cascading effects throughout, thereby producing phenotypic variability and the potential to diverge from the species-typical developmental trajectory.

As the organism develops within a species-typical environment or ontogenetic niche, the path toward species-typical preferences is guided and constrained by the context the young organism finds itself embedded within. The proposed mechanisms by which social and ecological experience is taken in and converted to neurological and behavioral outcomes has been described as a collaboration of opposing forces: a progressive process that broadens and sharpens perceptual functionality and a regressive process that narrows and tunes discriminative ability. Over time and repeated exposure to a particular set of environmental stimuli, both of these processes guide and constrain the development of species-typical perceptual preferences. The malleability of the young organism is reduced through these seemingly conflicting processes. According to Aslin and Pisoni (1980), sensory experience can have four different effects on development. First, sensory experience can induce the development of a new perceptual ability. Second, sensory experience can facilitate the further development of a currently immature sensory system. Third, continued sensory experience can maintain the optimum level of sensitivity for that particular environmental niche. Lastly, specific sensory impoverishment can lead to the decline of discriminative ability. While a substantial body of research has provided support for these first two predictions of developmental broadening, significantly less is known about developmental narrowing and what kinds of

experience contribute to the process. The current study aimed to explore the last two predictions of Aslin and Pisoni (1980) by attempting to hold the perceptual window open during prenatal development through stimulus enrichment. The studies outlined below are based on the hypothesis that if a young organism develops within a niche that provides atypically diverse sensory experience, then it will retain diverse sensitivity and therefore fail to develop species-typical perceptual preferences.

Beginning with the work of Gottlieb (1971) with precocial avian species, it became clear that socially-derived prenatal and early postnatal experience is a key mechanism for the emergence of species identification. Even without previous exposure to the maternal call of their own species, precocial chicks will typically prefer the maternal call of their own species. The seemingly prespecified emergence of this species-typical preference occurs through the embryo's active exposure with its own vocalizations and those of its siblings during prenatal development, which share certain acoustic features with the hen's maternal vocalization. How the narrowing of perception occurs to hone-in on these species-specific acoustic features and produce a species-typical preference is the focus of the current project.

With continued exposure to native stimuli over time, organisms become increasingly efficient in making nuanced distinctions between those native stimuli, at the expense of being able to distinguish between environmentally infrequent or novel permutations. The phenomenon occurs across stimulus classes and cross-modal perception, but most crucially in socially-pertinent domains such as face perception and communication (Scott, Pascalis, & Nelson, 2007). The phenomenon, referred to on the whole as "perceptual narrowing" is a domain-general pan-sensory process that occurs

throughout the lifespan, but most dramatically during prenatal and early postnatal development (Scott, Pascalis, & Nelson, 2007). The process of perceptual narrowing is a probabilistic selection process, whereby neural architecture interacts with environmental and self stimulation. Perceptual narrowing is not a process of discriminatory remembering or forgetting, but rather a process by which the organism gradually becomes unable to perceive or discriminate between sensory stimuli outside of a normally occurring ecologically-valid range.

Through perceptual narrowing, an organism becomes attuned to the most salient or regularly occurring features of their environment, pruning and allocating neuronal resources for increased efficiency (Kuhl & Rivera-Gaxiola, 2008; Nelson, 2001; Werker & Tees, 2005). This narrowing can be seen as a neural commitment to a particular environment, to a specific ontogenetic niche. Problems with perceptual narrowing can occur if the mature organism finds itself in an environment which requires perceptual discriminations that were lost during early development. Therefore, being able to “hold open” the perceptual window by consistent and diverse sensory enrichment may have benefits, including easier second-language acquisition in humans or the ability to identify individuals of other species.

CHAPTER II

LITERATURE REVIEW

Research on the regressive process of perceptual narrowing has provided convincing evidence for a domain general process that is both dependent on social input and anchored in neural architecture. The framework of Aslin and Pisoni (1980) and Gottlieb (1979) provided a model for perceptual “attunement” in which experience could induce, sharpen, and enhance perceptual discrimination of native stimuli, while simultaneously diminishing sensitivity to environmentally rare stimuli (Maurer & Werker, 2014). In accordance with developmental systems theory, the proposed perceptual narrowing mechanism combines top-down and bottom-up reciprocally determined interactions between brain, behavior, and the physical and social environment of the developing individual (Scott, Pascalis, & Nelson, 2007).

Perceptual Narrowing: A Domain General Social Cognitive Process

The term ‘perceptual narrowing’ has been used to explain a variety of regressive developmental phenomenon and has been defined both in terms of the underlying neural mechanisms as well as behavioral discrimination tasks. Perceptual narrowing can refer to any process in which the ability to discriminate between individual stimuli of a particular category changes as result of experience. Before exposure is amassed, there exists a broad range of stimuli that the organism can effectively discriminate; however this range gradually becomes more narrow and specific to environmentally relevant/prevalent features of stimulation (Lewkowicz, 2014; Scott, Pascalis, & Nelson, 2007). Environmentally irrelevant or rare permutations of a stimulus class are less attended to and the organism will eventually fail to make distinctions between them. On the basis of

the dynamic interactions among the brain, the active organism, and its environment, the individual organism becomes perceptually specialized and efficient, tailored for picking up relevant information from their particular surroundings (Lewkowicz, 2014; Scott, Pascalis, & Nelson, 2007).

Perceptual narrowing has been demonstrated in a variety of socially-salient sensory tasks with human infants, including but not limited to: phonetic and visual language discrimination and later language development (Kuhl, Stevens, Hayashi, Deguchi, Kiritani, & Iverson, 2006), facial recognition (Pascalis, Scott, Kelly, Shannon, Nicholson, Coleman, et al., 2005) intersensory redundancy perception (Lewkowicz & Ghazanfar, 2006), and culturally distinctive musical rhythms (Hannon & Trehub, 2005). Typically by the end of the first year, human infants have shifted from sensitivity to a wide range of sounds, rhythms, and faces to more efficient processing of specific characteristics of their native environment.

The proposed pan-sensory domain-general process is in direct opposition with traditional views of innate species-typical preferences and, in humans, the existence of a language-specific module or capacity, as it proposes a process that is necessarily dependent on environmental exposure and active experience (Maurer & Werker, 2014). The domain-general perceptual narrowing hypothesis is able to account for inter- and intra-individual change over time and across stimulus categories without resorting to the assumption of a genetically-determined or somehow “hardwired” mechanism.

Neurobiology of Perceptual Narrowing

Research into the possible neural substrates of perceptual narrowing has typically focused on either phonetic or facial recognition, as the quick temporal presentation of

sounds or images lends itself to neuroimaging methodology and measurement via event-related potentials (ERPs). Across these two domains a common pattern of neural response and subsequent change has emerged. These results supports the idea that perceptual narrowing co-occurs across the senses using the same or similar neural mechanism. Furthermore, research has indicated a connection between audio and visual perceptual narrowing; suggesting that combined audio-visual stimulation facilitates specification and neural commitment (Lewkowicz & Ghazanfar, 2006). However, it is currently unknown what kind of stimulation (i.e., unimodal or multimodal) most effectively facilitates altering the perceptual narrowing window. As perceptual narrowing occurs simultaneously across multiple modalities that are typically socially-derived (such as face and language perception) it has been suggested that perceptual narrowing occurs through the amodal properties of stimulation. Evolutionary psychologists have argued that since communication is paramount for human survival, perceptual narrowing through the amodal properties of stimulation must be the most efficient mechanism – pointing to the activation of the superior temporal sulcus in adults during tasks involving the synchronous processing of auditory and visual language processing (Pascalis, Loevenbruck, Quinn, Kandel, Tanaka, & Lee, 2014). However, no previous experiments have been conducted to address the claim that perceptual narrowing occurs primarily through amodal or modality specific properties during various points in perceptual development.

Longitudinal work on perceptual narrowing and phonetic discrimination was conducted by Rivera-Gaxiola, Silva-Pereyra and Kuhl (2005), in which they followed infants from 7- to 11-months old. At 7-months, infants' neural electrophysiological

response suggests equal ability to discriminate between native and non-native speech sounds; however as infants matured and exposure to their native language compounded over time, the neural response to discriminate non-native phonemes declined. This finding supports the gradual nature of the perceptual narrowing process. In another study, infants who displayed better neural native-language phonetic discrimination at 7.5 months were more linguistically advanced at 24-months, having a broader lexicon, creating more complex sentences, and longer mean length of utterances (MLU) (Kuhl, Conboy, Padden, Rivera-Gaxiola, & Nelson, 2008). Conversely, infants still discriminating among non-native phonemes at 7.5 months were less linguistically advanced at 24-months. Intriguingly, a comparison of prematurely born infants and full-term infants found that at 12-months post-partum, premature infants had a differential “electric mismatch [neural] response” while effectively discriminating non-native phonemes, indicating a lack of usual perceptual narrowing (Jansson-Verkasalo, Ruusuvirta, Huotilainen, Alku, et al., 2010). Later at 2-years-old, the premature infants continued to display language delays typical of their group.

Rand and Lahav (2014) suggest that pre-term infants typically experience some degree of linguistic delay or disability as a consequence of the atypical auditory environment of the Neonatal Intensive Care Unit (NICU). The altered perceptual milieu of the NICU contains a range of inorganic sounds may influence the perceptual narrowing process (Rand & Lahav, 2014). Rand and Lahav (2014) suggest that auditory enrichment only facilitates perceptual narrowing if that enrichment consists of stimuli that are ecologically valid, or rather a valid representation of the stimuli the organism will encounter in their future environment. Chipaux et al. (2013) found that infants born

prematurely had altered patterns of postnatal perceptual narrowing when comparing EEG responses to a human voice versus mechanical sounds. Infants born prematurely emitted the same characteristic “delta-brushes” in the auditory cortex up until 35 postmenstrual weeks; delta-brushes being indicative of immature sensory processing. Although the infants were born prematurely and had a history of stimulation outside of the womb, the delta-brushes in response to both ecologically valid and inorganic sounds were similar to those of an unborn fetus (Chipaux, et al., 2013). This indicates that there is some maturational threshold for perceptual narrowing that is not purely a function of postnatal auditory experience. Additionally, the in-utero environment acts like a buffer during this stage of prenatal sensory development; not having a sound attenuated environment can result in abnormal perceptual narrowing and future difficulty in language acquisition (Peña, Werker, & Dehaene-Lambert, 2012). Prenatally, the human fetus is exposed to speech sounds filtered through the mother’s body. These speech sounds do not offer the full frequency “broadcast range” as when travelling through air. Therefore, it has been suggested that preterm infants receive an enriched auditory enrichment by being able to experience unfiltered stimuli earlier in development. However, Peña, Werker, and Dehaene-Lambert (2012) found that preterm infants receive no linguistic advantages from earlier exposure to broadcast speech. Therefore, there is something uniquely beneficial about auditory exposure in-utero. These results suggest that while perceptual narrowing is a regressive process, it is not necessarily a “bad” process to be avoided – it provides the foundation for more sophisticated learning in specific environments.

The importance of social exposure and social interaction in perceptual narrowing and, consequently, future language development, has also been explored using ERP

methodology. For example, the ability of a 9-month old infant to discriminate non-native (Spanish) phonemes and words at the neural level was predicted by the relative richness of previous social interaction with a tutor speaking the non-native language (Conboy, Brooks, Meltzoff, & Kuhl, 2008). Results of neural activation patterns and behavioral discrimination tasks in cross-species facial recognition and multisensory face/voice agreement tasks are comparable. Six-month-old infants showed the same neural discrimination activations for monkey and human faces (de Haan, Pascalis, & Johnson, 2002). Lewkowicz and Ghazanfar (2009) found that not only can newborn and 4-month-old human infants effectively discriminate individual monkeys on the basis of nuanced facial features but they can also successfully match seemingly indistinguishable monkey vocalizations to the corresponding facial articulation. This skill is lost by infants at 12 months reared, traditionally, in the absence of non-human primates. This ability to discriminate between species is not limited to primates; young infants can also successfully match canine faces with the appropriate canine vocalizations (Quinn & Eimas, 1996) as well as successfully discriminate between individual sheep faces (Simpson, Varga, Frick, & Frigaszy, 2010). The connection between facial and phoneme perceptual narrowing and memory are thought to be the result of the multimodal synchronous stimulation found in social interaction. Positron Emission Tomography (PET) research has demonstrated that 2-month old infants have adult-like neural activation in typical language regions during a face-recognition task, suggesting an early link between the audio and visual systems (Tzourio-Mazoyer et al., 2002).

In comparing neurological responses of infant and adult humans to non-native phonemes, Bosseler et al. (2013) found significant differences in brain waves associated

with cognitive effort and attention required to make these distinctions. Six month old infants showed no significant difference in brain oscillations, as measured by magnetoencephalography (MEG), when presented with native versus non-native phonemes, whereas adults showed increases in neurological effort when attempting to perceive non-native distinctions. The increase in effort required to perceive non-native phonemes is indicative of a developmental history wherein these distinctions were not present or important. Additionally, a third group of 12 month old infants displayed oscillation patterns closer to adults than to their 6 month old counterparts, indicating that perceptual narrowing rapidly occurs during this period so much so that the infant approximates adult perception at 1 year (Bosseler et al., 2013).

The neurological findings regarding perceptual narrowing are often incongruent with behavioral tasks; results usually indicate a faster decline in behavioral performance in non-native phoneme and word discrimination tasks than in observed neurological responses (Rivera-Gaxiola, Silva-Pereyra, & Kuhl, 2005; Scott, Shannon, & Nelson, 2006). Infants typically stop behaviorally responding (typically eye gaze shifting) to non-native distinctions, even if the discrimination is still being exhibited neurologically. This implies that the neural substrate is preceded by and may be dependent on behavior and the contingencies encountered in the social environment. While findings from neuroscience are able to demonstrate how one aspect of the perceptual narrowing mechanism functions, the neural responses to native and non-native stimulus discrimination tasks are in-and-of themselves less informative of perceptual narrowing unless paired with behavioral changes.

Perceptual Narrowing & Human Speech Perception

Kuhl's (2004) native language neural commitment (NLNC) hypothesis has provided a useful framework for perceptual narrowing as it applies to language development. The NLNC hypothesis states that as infants mature, they become increasingly efficient at making nuanced distinctions between native phonemes, while non-native distinctions meld together. According to the NLNC, infants unconsciously "compute" the prevalence or scarcity of stimulus features (i.e., phonemes) in the environment, which then allows the infant to learn the structure of a particular language in order to form words and, eventually, sentences (Kuhl, 2004). Therefore, while infants have a universal ability to learn any human language, that ability deteriorates as experience within a particular linguistic environment is amassed.

Relatively little is known about perceptual narrowing as a function of prenatal and early postnatal experience. Seminal work on behavioral perceptual narrowing in language conducted by Werker and Tees (1984) demonstrated a stark decline between 6- and 12-months of age in the ability of monolingual English infants to distinguish characteristic /Da/ and /da/ phonemes found in Hindi. Infants were trained to turn their head 90 degrees when a different phoneme was played after habituation to one repeated phoneme; the phoneme switch preceded the presentation of an entertaining toy to the side of the infant. American infants at 6-months could make the difficult distinction between the non-native Hindi sounds and were therefore able to correctly alter their head positions to view the entertaining event. However, at twelve months, infants failed to reliably turn their heads, indicating that they no longer noticed the difference between the /Da/ and /da/ phonemes (Werker & Tees, 1984).

More recent work not only suggests that increasing experience results a decline in the ability to differentiate non-native contrasts, but in turn facilitates the more nuanced distinctions made between native phonemes (Kuhl & Rivera-Gaxiola, 2008; Werker & Tees, 2005). Likewise, infants in this window of perceptual sensitivity are simultaneously losing the ability to distinguish among faces from other ethnic groups (Kelly, Quinn, Slater, Lee, Ge, & Pascalis, 2007) and have increasing difficulty identifying metric changes in music from outside their immediate environment (Hannon & Trehub, 2005).

Not only do infants rapidly lose the ability to make non-native contrasts of human language sounds, they also lose the ability to distinguish between the voices of individuals. Friendly, Rendall, and Trainor (2013A) found that between 6 and 12 months, human infants lose the ability to distinguish between two voices of a non-human primate species (rhesus monkeys). That is, withholding the rhythmic properties of the primate calls, the 12-month old infants could not use the auditory-only properties such as pitch or timbre to effectively discriminate between two individual rhesus monkeys; something they were able to do 6 months prior. However, it seems with neurological plasticity, not all is lost to perceptual narrowing. In a follow up study, Friendly, Rendall, and Trainor (2013B) were able to temporarily increase the older infants' ability to distinguish the voices of foreign species through a 2-week monkey-voice training procedure. Through repeatedly exposing 12-month old infants to a narrative involving multiple, individually labeled monkey voices, Friendly, Rendall, and Trainor (2013B) were able effectively "reverse" perceptual narrowing for this specific stimulus set. Not only did these trained 12-month old infants successfully discriminate the monkey voices, but they outperformed the untrained 6- month old participants. While perceptual narrowing is a rapid process, it

seems that certain types of stimulus exposure or environmental enrichment can reopen the perceptual window.

Perceptual narrowing is a socially guided process, the amount, variety, and quality of stimulus exposure can alter the progression of discrimination abilities in early development. One factor that has been shown to impact individual variation in perceptual narrowing is the quality of mother-child postnatal interactions, whether those interactions are largely passive or contingent may be a determining factor for the speed at which perceptual narrowing occurs. Elsabbagh et al. (2013) classified mother-infant dyads as either “high-contingency” or “moderate-contingency” based on monitored play sessions. As previous studies indicated that perceptual narrowing of human infants resulted in a failure to make non-native distinctions around 10 months, Elsabbagh et al., (2013) found that infants that had more contingent (versus passive) linguistic interaction with their mothers had accelerated perceptual narrowing. At 6 months, infants from high-contingency dyads failed to make non-native contrasts, an indicator that perceptual narrowing has occurred, whereas infants from moderate-contingency dyads continued to make non-native contrasts up until 10 months. Perceptual narrowing, as a socially interactive process, seems to rely on a variety of properties of stimulation, not just simply overall quantity.

Although external environmental experience is imperative to perceptual narrowing, evidence suggests that self-stimulation is also important for both adult and infant humans’ ability to make native versus non-native phoneme distinctions. The Articulatory Organ hypothesis posits that through self-stimulation (i.e., babbling) infants narrow in on native contrasts by the end of their first year. Best and McRoberts (2003)

tested the ability of monolingual English infants to discriminate between non-native (Zulu, Tigrinya) contrasts, depending on if those phonemes used the same or different articulatory organs to produce. Younger infants (6-8 months) could reliably discriminate between non-native phonemes that use the same articulatory organ (larynx), a difficult task. Older 10-12 month old infants could not make the distinction between these “within-organ” non-native phonemes. However older infants (Best & McRoberts, 2003) and adults (Best, McRoberts, & Goodell, 2001) could still make non-native distinctions if the phonemes presented used different articulatory organs to produce (tongue versus lips). This suggests that perceptual narrowing is not just facilitated by external auditory exposure, but also expression and the redundant sensory information (auditory and vestibular) speech production provides.

Perhaps the most compelling evidence towards a pan-sensory domain-general perceptual narrowing process comes from Lewkowicz and Ghazanfar (2009), who argue that perceptual narrowing contributes to the development of multisensory systems through exposure to socio-ecologically valid intersensory redundancies. In their cross-sectional study of 4-, 6-, 8-, and 10-month old infants, they found that 4- and 6-month old infants had the ability to discriminate cross-species audio-visual pairings (monkey calls and corresponding monkey face articulations), whereas older infants could not. Pons, Lewkowicz, Soto-Faraco, and Sebastian-Galles (2009) conducted a follow-up using monolingual English and Spanish infants in English versus Spanish audio and visual discrimination task and found similar results.

Non-native stimulus experience in later infancy can have an effect on later non-native distinctions if the quality of social interaction is rich and sustained. For example,

Kuhl, Tsao, and Liu, (2003) demonstrated that perceptual narrowing may be somewhat reversible. Nine-month-old monolingual-English infants were given many play sessions with a Mandarin Chinese speaker and subsequently were better at making phonetic distinctions in Mandarin than controls. In the same study, Kuhl et al. (2003) found that social interaction matters, as non-native stimulus exposure via audiovisual equipment did not have the same delaying effect on perceptual narrowing. This provides evidence that perceptual narrowing requires constant and consistent facilitation and maintenance from native stimulus classes, but can also be modified in reaction to later non-native stimulus exposure. Furthermore, Scott, Pascalis, and Nelson (2007) have suggested that the previously neglected neural architecture for discriminating non-native stimuli can be fostered and resume functionality given appropriate social enrichment. The ERP research on perceptual narrowing suggests that even after behavioral discriminations dissolve, the neural architecture to make these distinctions may not be erased or destroyed, but rather could remain dormant. Therefore, frequent, regimented exposure with social feedback to non-native audio, visual, or taste stimuli, can “reverse” perceptual narrowing to some extent.

The Black Box of Prenatal Development

In humans, both monolingual and bilingual newborns show the ability to discriminate between and display preferences for languages they were exposed to in-utero (Byers-Heinlein, Burns, & Werker, 2010; Nazzi, Bertoncini, & Mehler, 1998). Even before birth, the human fetus can exhibit physiological responses to familiar versus novel patterns in maternal speech. DeCasper, Lecanuet, Busnel, Granier-Deferre, and Maugeais (1994) found that human fetuses in the third trimester were able to distinguish

between a short rhyme repeated by the mother from 33 to 37 weeks and a novel rhyme. The measure of reaction to the familiar rhyme was a significant cardiac deceleration; DeCasper et al. (1994) supposed the slowing of heart rate was indicative of the fetus' selective attention to that particular rhythmic pattern – which in turn promotes additional learning. Even earlier in prenatal development, preterm human fetuses have been shown to make these distinctions in auditory pattern. Krueger, Holditch-Davis, Quint, and DeCasper (2004) instructed mothers to recite a nursery rhyme twice a day starting at either 28-weeks or 32-weeks gestation. The timing of the onset of stimulus exposure, either before or after a notable maturation in the autonomic nervous system, resulted in the younger fetuses needing substantially more time to learn the familiar rhythmic pattern. Therefore, there appears to be interaction between stimulus onset, amount of exposure, and physiological maturation on the ability to differentiate familiar versus novel stimuli.

The effect of prenatal stimulation on postnatal auditory preferences has traditionally been shown for maternal speech pattern, rhythm, and prosody. However, perceptual narrowing has been shown to occur through the modality specific acoustic properties of stimulation, such as pitch. Partanen, Kujala, Näätänen, Liitola, Sambeth, and Huotilainen (2013) instructed expectant mothers to repeat a trisyllabic pseudoword (“tatata”) with occasional variations in pitch and middle syllable sound (“tatota”) starting at 29 weeks gestation. Postnatal neural testing of infants in the learning condition indicated that they could correctly make distinctions between the pitch of two utterances of “tatata”, whereas controls did not display this discrimination ability. However, both enriched and control infants could discriminate between the more obvious

differences in middle syllable switch (“tatata” vs. “tatota”). Infants that received the augmented prenatal exposure were not only able to detect the nuanced pitch distinctions, but also generalized to include changes in vowel duration and intensity (Partanena et al., 2013). Therefore, prenatal auditory enrichment affected the infants’ ability to make distinctions for both the amodal (intensity, duration) and modality specific (pitch, phonation) properties of speech sounds.

Both gestational age and postnatal age have been shown to alter how infants perceive speech sounds of their native language. Key, Lambert, Aschner, and Maitre (2012) examined the effects of both gestational age and postnatal age of human infants in the NICU. When comparing infants born between 24-40 weeks gestation on auditory ERPs for native phoneme contrasts, Key et al. (2012) found a threshold for prenatal development. Overall, as the infant accrues experience postnatally, it becomes more adept at making native phoneme contrasts, older infants displaying neurological responses in line with correct discrimination of those speech sounds. However, infants born at or before 30 weeks of gestation could not reliably make those same distinctions compared to counterparts with the same postnatal age. Key et al. (2012) suggest that a minimum level of brain maturity at birth is required for postnatal experience to impact perceptual narrowing and, in turn, milestones of language acquisition.

Prenatal language experience has been shown to influence the neonatal neurological response of human infants when comparing the familiarized language they were exposed to prenatally versus a novel language or non-language sounds. Using Near-infrared spectroscopy (NIRS), May, Byers-Heinlein, Gervain, and Weker (2011) compared neurological activation responses of 0-3 day old full-term neonates to familiar

(English) versus unfamiliar (Tagalog) speech, in both forward (natural) and backward (non-linguistic) recordings. Results indicated that human newborns attended more closely to the language they had previous experience with, having significantly higher levels of oxygenated blood overall when listening to the native language. May et al. (2011) conclude that prenatal auditory experience has a significant effect on brain response and prenatal experience already has the newborn “tuned in” to a specific language environment.

Abnormalities in the perceptual narrowing process have been shown in human infants born prematurely, with deficiencies in the initial perceptual narrowing process cascading into future impairment in language acquisition. Whereas infants born full-term showed a gradual loss in non-native phoneme distinction between 6-12 months, prematurely born infants retained the ability to make those discriminations at one year (Jansson-Verkasalo, Ruusuvirta, Huotilainen, Alku, Kushnerenko, Suominen et al, 2010; Krueger, Holditch-Davis, Quint, & DeCasper, 2004). The lack of native phoneme specialization in premature infants at 12 months predicted significant language delays at two years. Human infants and children typically show such quick and seemingly effortless language acquisition that many argue that it is innate akin to species-typical preferences and behaviors. However, disturbances in perceptual narrowing found in premature infants have been shown to make future language acquisition systematically difficult, suggesting that it is the result of a process dependent on prenatal environmental experience.

Comparative Based Research

Prenatal studies in human language development are few and far between. However, a variety of comparative-based research has demonstrated the influence of prenatal stimulation on later species-typical perceptual preferences. Research of avian in-ovo heart-rate and behavioral changes in response to species-typical stimulation corroborates the results from the human in-utero studies. Chicken, duck, and quail embryos that have moved into the airspace of the egg prior to hatch exhibit increased bill- or beak-clapping and heart rate augmentation in response to species-specific maternal calls (Heaton & Galleher, 1981; Gottlieb, 1965). Additionally, artificially increasing heart rate by injection of norepinephrine has been shown to impair perceptual learning in bobwhite quail embryos, making them unable to identify a familiarized maternal call (Markham, Toth, & Lickliter, 2007). Arousal that results from confounding stimulation has also resulted in impaired prenatal perceptual learning and memory. Bobwhite quail embryos exposed to asynchronous auditory/visual stimulation had increased heart rate and arousal compared to those who received auditory-only or synchronous auditory/visual stimulation (Reynolds & Lickliter, 2001). Increased arousal levels during late perceptual development have been shown to be detrimental to learning and memory of a species-specific maternal call (Lickliter & Hellwell, 1992).

The importance of direct social interaction in perceptual narrowing and communication development has been demonstrated in humans as well as several species of songbirds (Doupe & Kuhl, 1999). Avian species and humans share many commonalities in auditory system development, including a similar pathway of auditory feedback for self-stimulation and the perception of conspecific vocalizations.

Neurological parallels in language development and auditory learning also exist between humans and avian species, respectively. These similarities include the left hemispheric canalization of language in adults and a hierarchically organized forebrain area which coordinates motor and auditory functions (Doupe & Kuhl, 1999). More pertinent for the current study, both humans and avian species have similar sensitive periods for perceptual learning, a developmental window wherein the organism can distinguish all permutations of a stimulus class and which quickly diminishes over early development with increased exposure (Doupe & Kuhl, 1999; Volman, 1993). Due to the similarities between birdsong and human language, and because of birds' encapsulated prenatal environment, a number of avian species have been used to investigate how auditory and visual patterns can be learned or disrupted by manipulating prenatal experience.

Gottlieb's (1971) seminal work on the species identification (imprinting) of precocial birds revealed the particular perinatal conditions determine species-specific auditory preferences. Maternal, sibling, and self-stimulation are all parts of the ecological context in which species-typical preferences and behavior emerge. For example, mallard duck embryos denied peer and self-stimulation through isolation and the paralysis of their vocal chords fail to develop a species-specific preference for the maternal call of their species (Gottlieb, 1971, 1978, 1984; Gottlieb & Vandenberg, 1968). Of particular interest to perceptual narrowing was the finding that the devocalized duck embryos became more malleable, more receptive to learning and preferring the maternal call of a different species (domestic chicken) after repeated exposure (Gottlieb, 1991). Similarly, bobwhite quail chicks who receive exposure to a Japanese quail call passively prenatally and then had a brief contingent training session postnatally redirected their species-

typical auditory preference to prefer the Japanese quail call over a bobwhite maternal call, an exceptionally difficult task (Harshaw & Lickliter, 2010).

Visual imprinting operates under the same contextual determinants; for example the emergence of a species-specific visual preference for a conspecific hen requires unconstrained experience with siblings (Lickliter, 1991). Bobwhite quail chicks reared postnally in social isolation or in a peer group consisting of several different quail species fail to recognize and prefer the hen of their species. These contextual determinants also occur across sense modalities; a lack of tactile stimulation resulting from isolated incubation has been shown to moderate the learning of a maternal call and maternal visual cues in bobwhite quail chicks (Lickliter & Lewkowicz, 1995; Sleigh & Lickliter, 1998). The order, timing, and schedule of exposure all appear to be involved in the successful emergence and development of species-typical preferences and behavior.

Neurological studies of perceptual learning in precocial birds have examined the different mechanisms that could mediate the interaction between environmental stimulation, neurophysiology, hormones, and behavior. For example, prenatal auditory enrichment has been shown to increase the number, size, and complexity of neurons in domestic chickens, regardless if the enrichment was comprised of normally occurring stimulation (Wadhwa, Anand, & Bhowmick, 1998). Chaudhury & Wadhwa (2009) detailed how different proteins involved in the development of the auditory pathway and hippocampus of domestic chickens are influenced by prenatal auditory stimulation, both ecologically valid calls and nonstandard sitar music. Starting on day 10 of incubation (out of a 21-day incubation period), chick embryos were exposed to either a maternal call or sitar music 10 min/hr, every hour until hatch. Throughout development, the expression of

two proteins (cyclic adenosine monophosphate-response element binding (CREB) and brain-derived neurotrophic factor (BDNF) associated with neural survival, dendritic arborization, and the regulation of synaptic strength were assessed. Both auditory enriched groups displayed patterns of CREB and BDNF consistent with heightened learning and memory; however chicks were not subsequently tested behaviorally for a preference. The same protocol also yielded results indicating an increase in anti-apoptotic proteins, Bcl-2 and Bax, in auditory enriched groups; therefore auditory enriched groups had less neuronal death and increased differentiation of the auditory nuclei (Alladi, Roy, Singh, & Wadhwa, 2005A). Although chicks from the music enriched groups reflected many neurobiological benefits compared to controls, species-specific prenatal auditory enrichment had markedly stronger improvements compared to musical enrichment (Panicker, Wadhwa, & Roy, 2002).

If perceptual narrowing is a domain-general pan-sensory process, it makes sense that the process would be evident across a range of species (Doupe & Kuhl, 1999). While perceptual narrowing has been shown to have already begun prenatally, little is known about whether and to what extent perceptual narrowing could be delayed, essentially holding open the perceptual window into later development. Retaining the initial malleability of sensory discrimination could be beneficial in making adjustments to potential future environments. What type of prenatal exposure (or lack of exposure) can influence perceptual narrowing and consequently later behavioral development? What other stimulus classes could be affected by prenatal exposure? By better understanding the perceptual narrowing process the developmental roots of species-typical preferences and behavior can be better understood.

Enrichment, Perceptual Narrowing, & Response to Novelty

Environmental Enrichment (EE) has been shown to have profound epigenetic, neurological, and behavioral effects, particularly when applied to the rearing environments of young organisms (Baroncelli, Braschi, Spolidoro, Begenisic, Sale, & Maffei, 2010). Providing exposure to diverse stimuli early in development can change the organism's reactivity toward novel stimuli both physiologically and behaviorally, both immediately and distally. Even prenatal environmental enrichment can have long lasting effects on response to stress and novelty into adulthood (Cymerblit-Sabbaa, Lasri, Gruperc, Aga-Mizrachia, Zubedata, & Avital, 2013). In terms of perceptual narrowing, early enriched rearing paradigms have been shown to alter neural plasticity and response to non-native auditory and visual stimuli, even if those stimuli were not part of the original enriched environment.

Prenatal auditory enrichment in the form of music has been shown to alter neurophysiology in both avian and mammalian models, including domestic chickens in-ovo and rats in-utero. As previously discussed, domestic chicken embryos receiving prenatal auditory enrichment in the form of complex sitar music showed a variety of neurological differences, including the expression of transcription factors associated with regeneration in the brainstem auditory nucleus (Alladi, Roy, Singh, & Wadhwa, 2005B) more complex hippocampal development (Chaudhury & Wadhwa, 2009; Wadhwa, Anand, & Bhowmick, 1998) and the presence of proteins associated with neural survival (Alladi, Roy, Singh, & Wadhwa, 2005A). Similarly, rat embryos that received music in-utero demonstrated increased neurogenesis in the hippocampus as well as significantly better performance in tests of spatial ability and emotional reactivity (Kim et al., 2006).

However, the type of prenatal auditory enrichment was crucial; rats exposed to louder, mechanical sounds performed significantly poorer compared to controls and music enriched rats. Xu, Yu, Cai, Zhang, and Sun (2009) found that rats that received prenatal auditory enrichment in the form of music had altered levels of protein expression in the auditory nucleus that translated into significantly better performance in postnatal auditory discrimination tasks. The authors attribute the enriched rats' behavioral performance to increased neural plasticity.

Previous attempts to artificially provide prenatal auditory enrichment have been somewhat successful, but due to practical limitations have not been prevalent. Blum (1998) provided standardized redundant auditory-vestibular stimulation in a program he termed "Leonardo 180" to expectant mothers and their developing fetuses from 16 weeks to 24 weeks gestation. The program consisted of a series of vocal and instrumental musical pieces which had lower frequencies and slower rhythms early in development and became increasing complex through the course of the program. Not only did the musical pieces change in acoustic features over development, but also represented a variety of cultures and time periods. Results indicating that those infants that received prenatal auditory-vestibular enrichment performed better on measures of sensorimotor development postnatally, including the onset of monosyllabic babbling, one of the first indicators of language acquisition (Blum, 1998). Similarly, Panthuraamphorn, Dookchitra, and Sanmaneecha (1999) found that prenatal auditory and vestibular enrichment consisting of both maternal voice and musical stimulation increased postnatal responsiveness to stimuli. Although infants demonstrated a preference for all familiar stimuli including maternal voice, music, heartbeat, rhythmic patting, and rocking pattern,

when comparing the familiar acoustic stimuli of maternal voice versus music, infants showed a stronger preference for their mother's voice. This finding suggests that ecologically valid forms of auditory stimulation are more salient than those that are contrived.

Instead of adding artificial stimulation, the effect of prenatal auditory enrichment in humans has been demonstrated in newborn human infants who are organically exposed to multiple first languages in-utero. The co-acquisition of multiple first languages in humans is shaped by prenatal auditory and redundant audio-vestibular stimulation, preparing them not only to learn the languages originally presented, but also to have increased sensitivity to novelty postnatally. Byers-Heinlein, Burns, and Werker (2010) conducted discrimination and preference tests with newborns exposed prenatally to either English only, Tagalog only, English and Tagalog, or English and Chinese. Results indicated that newborns that received a variety of language sounds from two languages prenatally had altered patterns of perceptual narrowing. Monolingual infants had a robust preference for their native language postnatally, whereas bilingual infants showed no significant preference for either native language (Byers-Heinlein, Burns, & Werker, 2010). This effect was not limited to the languages present in the original stimulation, however. The newborns exposed to English and Chinese in-utero demonstrated a significant preference for Tagalog, a novel language, indicating a broader perceptual range and openness to new experience. Additionally, the authors argue that the rhythmic similarities between Chinese and Tagalog were imperative for fostering the preference for the novel language (Byers-Heinlein, Burns, & Werker, 2010). The differences in perceptual narrowing of bilingual infants may also cascade into perceptual and cognitive

advantages into adulthood (Werker, 2012); if the environment maintains the broadened perceptual narrowing window through consistently providing this increased variation.

Petitto et al. (2012) looked at bilingual infants' brain response to non-native phoneme contrasts across age groups that typically corresponded to milestones in perceptual narrowing (4-6 and 10-12 months). Using fNIRS imaging, Petitto et al., (2012) found that bilingual infants showed neural response indicative of phoneme distinctions for a novel language much up through 10-12 months, wherein monolingual infants fail to make such a response. The authors suggest that infants that coacquire multiple first languages have altered neurological and behavioral language processing that is advantageous when confronted with novelty later in development. The increased variability the infant experiences in the perinatal environment prolongs malleability, keeping the perceptual narrowing window "open" significantly later in development. Petitto et al., (2012) named this phenomenon the "perceptual wedge", wherein multiple languages figuratively hold open the perceptual window. Therefore, auditory enrichment not only prevents a preference from forming between the stimuli provided, but also generalizes to include differential response to novelty.

Infants that co-acquire multiple first languages are tasked with specializing in several languages simultaneously. Therefore, bilingual children and adults must also go through a process of perceptual narrowing. Due to the increased variation these individuals are exposed to regularly, they might not reach the same perceptual restriction as monolinguals (Byers-Heinlein & Fennel, 2013). The lifelong altered perceptual narrowing window is a function both of the prenatal and early postnatal auditory enrichment as well as life-long maintenance of that widened perceptual narrowing

window by speaking multiple languages with regularity. Without enduring maintenance of the altered perceptual narrowing window, sensitivity will begin to decline in response to the decreased variability experienced in the environment.

In older humans, musicians have received attention because of their unique patterns of perceptual narrowing; being able to detect nuanced differences in various acoustic properties. Strait and Kraus (2014) provide an analysis of musicians as the model organism for studying experience-dependent neuroplasticity as it relates to auditory learning. Musical training in later development serves as a form of auditory enrichment in which musicians are able to learn these fine distinctions between non-linguistic sounds (Strait & Kraus, 2014). For example, preschool children with musical training are much more efficient and precise when discriminating commonly confused speech sounds compared to those children without such enrichment. These preschool musicians also have enhanced auditory brainstem function, in parallel to the above animal research. Musical enrichment provides positive cascading effects on other forms of auditory processing, including language and multisensory processing, across the lifespan. Adults that received musical training early in life have been shown to suffer less deterioration of auditory function as they age. While musical or linguistic learning is possible into adulthood, Strait and Kraus (2014) infer, as many others, that the earlier the better.

Intersensory Redundancy and Perinatal Auditory Learning

Across species perceptual narrowing is likely the result of interactions between various contextual determinants. The amount, type, frequency, and duration of stimulation, along with the environmental context in which stimulation occurs, can affect

the organism neurologically, physiologically, and behaviorally. Socially-derived stimulation is an inherently rich source of information due to the multimodal, redundant nature of social interaction. Social interaction with parents, siblings, or self-stimulation includes synchronous auditory, visual, and tactile/vestibular information. For example, a hen sitting on eggs produces paired auditory and vestibular stimulation to her eggs, just as a human mother produces paired auditory and vestibular stimulation to her fetus when she speaks. The postnatal environment of precocial birds and humans introduces visual cues synchronous with auditory stimulation. This synchronous multimodal stimulation, referred to as intersensory redundancy, can facilitate or hinder different kinds of perceptual learning by amplifying different properties of stimulation. If intersensory redundancy can enhance perceptual learning and memory, it might also be able to keep the perceptual window from narrowing by more effectively highlighting features and properties of non-native stimuli.

Intersensory redundancy has been shown to facilitate perceptual learning across birds and mammals. Both animal and human infants are particularly adept at attending to amodal information early in development, since amodal information, such as intensity, tempo, and frequency, is present across sense modalities and can therefore be perceived concurrently. The synchronous pairing of two (or more) sense modalities recruits selective attention, thereby improving subsequent learning and memory (Bahrick & Lickliter, 2000; Lickliter, Bahrick, & Honeycutt, 2004).

In humans, intersensory redundancy has been shown to improve discrimination and retention of amodal information, both for social and non-social events. Flom and Bahrick (2007) found that infants at four-months could discriminate different affect in a

woman model if the auditory and visual presentation was synchronous. In non-social events, such as a hammer hitting a surface, similar results have been found. Younger infants are able to detect changes in the amodal properties of rhythm and tempo only in synchronous auditory-visual presentations; by eight-months infants are able to detect these changes in both auditory/visual synchronous and unimodal presentations (Bahrick & Lickliter, 2004). Although intersensory redundancy can facilitate learning of amodal properties in early perceptual development, it is at the cost of discriminating modality-specific stimulus properties. For example, three-month old infants presented with an auditory/visual synchronous presentation of a female model are not able to detect changes in voice pitch; whereas those three-month-olds given auditory-only experience are able to make the pitch distinction (Bahrick, Lickliter, Shuman, Batista, Castellanos, & Newell, 2005). The majority of intersensory redundancy work on human subjects has been conducted with infants three-months old or older; this allows for a rich postnatal history of exposure to both social and non-social redundancies in the environment prior to testing. The use of precocial birds, such as the bobwhite quail, allows research into the effect of prenatal stimulation on learning and behavior, with the ability to measure preference or discrimination as soon as the day after hatching.

Prenatally, bobwhite quail embryos exposed to redundant auditory/visual stimulation consisting of a maternal call paired with a pulsing light synchronous with each note of the call demonstrated enhanced perceptual learning of the call; quail chicks who received synchronous auditory/visual exposure were able to learn the call variant in 1/4th the time and remember the call four times as long compared to groups receiving only auditory or asynchronous auditory-visual presentations (Lickliter, Bahrick, &

Honeycutt, 2002, 2004) Additionally, the bimodal synchronous onset of the stimulus has been shown to recruit attention. Jaime, Bahrick, and Lickliter (2010) found that pairing only the first burst of the five-note maternal call with a synchronous light flash was sufficient to enhance perceptual learning and memory.

Although synchronous bimodal experience has been shown to facilitate perceptual learning, it does so only for the amodal properties of the stimulus pair – the properties which both modalities share, such as tempo, duration, and intensity. Intersensory redundancy has been shown to effectively interfere with the learning of modality specific properties, especially in early development or when the perceptual task is difficult (Vaillant, Bahrick, & Lickliter, 2009; Vaillant, 2012). For example, bobwhite quail embryos exposed to a maternal call variant unimodally (audio only) were able to detect a subtle change in pitch and prefer the call they were originally exposed to, whereas quail embryos that received redundant auditory and visual stimulation were unable to detect the altered pitch. Similarly, Radell and Gottlieb (1992) found that too much redundant stimulation can interfere with prenatal learning of a species typical maternal call. When duck embryos received intense redundant auditory and vestibular presentation of a maternal call variant prenatally, they did not demonstrate a postnatal preference. Radell and Gottlieb (1992) later reduced the intensity of the vibration that accompanied the auditory stimulation and ducklings were then able to learn and remember the call variant postnatally. Therefore, redundant bimodal stimulation that is too intense may interfere more with selective attention or arousal, making it difficult for the embryo to benefit from both the amodal and modality specific properties of stimulation. As the organism gains more experience and becomes more adept at detecting nuances in native stimuli, it

can detect both amodal and modality specific properties to make perceptual discriminations, across multimodal and unimodal stimulus presentations.

Whether perceptual narrowing occurs primarily through the detection and selection of amodal properties (i.e., rhythmic pattern) or modality specific properties (i.e., pitch) is largely unknown. Gottlieb's (1978) work on mallard ducks suggests that the repetition rate (amodal property) is an important feature in the young's ability to hone in on species-specific vocalizations; however, Gottlieb's (1980) research on wood ducks suggests the frequency modulation (modality specific acoustic property) is important for species identification for that species. Research on human infants is equally divided, suggesting that both rhythm and phonetic sound are features of language development that rely on perceptual narrowing. Thus, the current project addressed what features of auditory stimulation, amodal or modality-specific may be more important to the prenatal sensory attunement process. Specifically, the following study explored whether (1) the perceptual narrowing window can be extended through prenatal auditory enrichment, (2) how prenatal auditory enrichment can affect response to novelty in the same stimulus class, and (3) whether the discrimination of amodal or modality specific properties may narrow first in early development.

Figure 1

Model of Perinatal Perceptual Attunement

| Onset of Auditory Function | | Prenatal Experience | Early Postnatal Preference | Postnatal Experience | Postnatal Preference |
|--|-------------------|--|----------------------------|--|----------------------|
| <div>Broad Perceptual Sensitivity</div> <div><div></div></div> | Previous Research | <u>No Manipulated Stimulation</u> Self-Stimulation Broodmates | Species-typical | <u>No Manipulated Stimulation</u> Self-Stimulation Broodmates | Species-typical |
| | | <u>Impoverished Environment</u> Paralysis of vocal chords Social Isolation | Malleable / None | <u>Manipulated Stimulation</u> Species-atypical Passive Exposure | Species-atypical |
| | | <u>Species-atypical</u> Passive auditory exposure to one alternative call | Malleable / None | <u>Manipulated Stimulation</u> Species-atypical Contingency Training | Species-atypical |
| | Current Study | <u>Enriched Environment</u> Passive auditory exposure to a variety of alternative calls | Malleable / None | <u>No Manipulated Stimulation</u> Self-Stimulation Broodmates | Species-typical |
| | | <u>Enriched Environment</u> Passive auditory exposure to a variety of alternative calls | Open to Novelty | <u>No Manipulated Stimulation</u> Self-Stimulation Broodmates | Species-typical |
| | | <u>Enriched Environment</u> Passive multimodal exposure to a variety of alternative calls | Malleable / None | <u>No Manipulated Stimulation</u> Self-Stimulation Broodmates | Malleable / None |
| TIME <div><div></div></div> | | | | | |

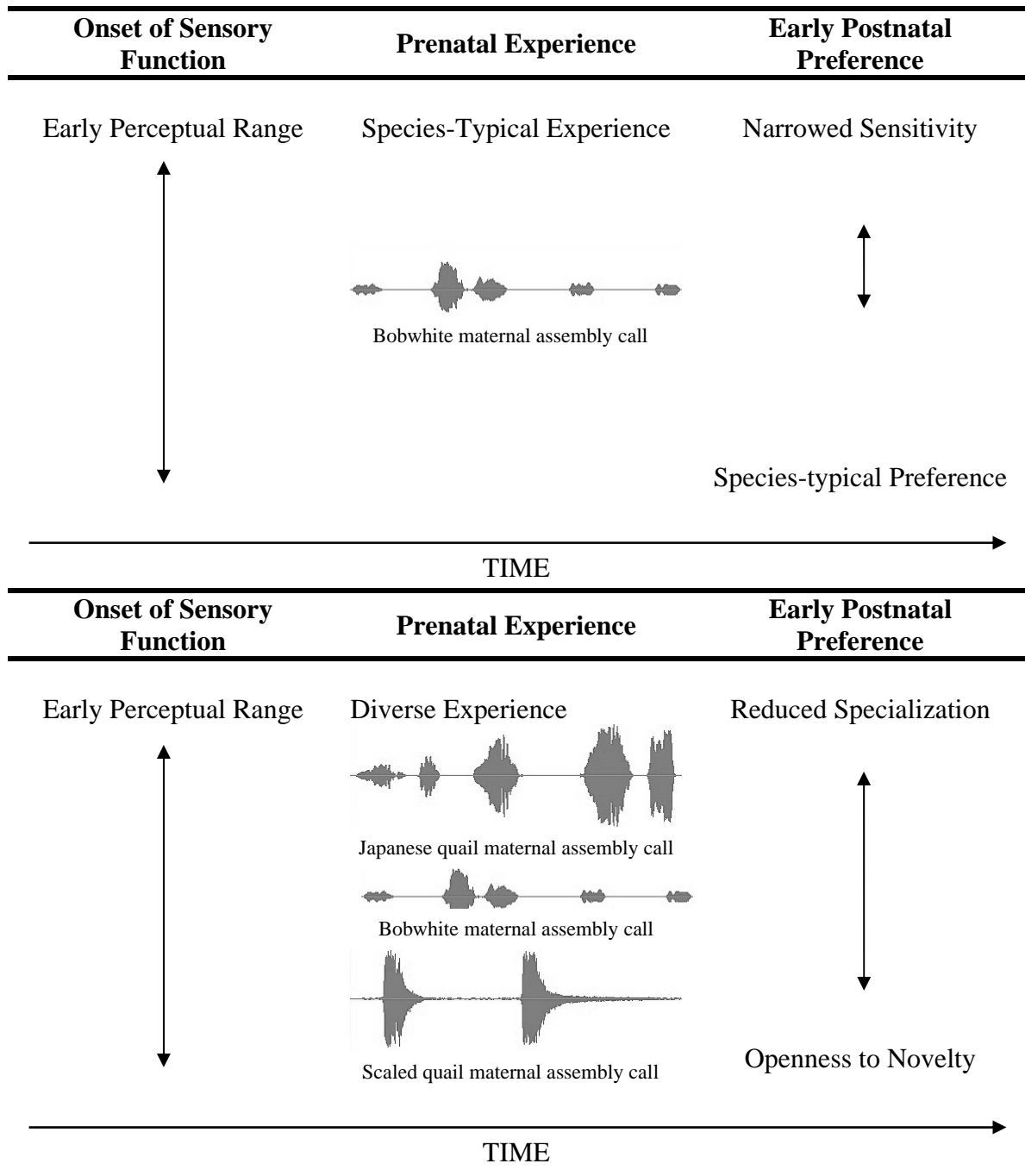
CHAPTER III

RESEARCH DESIGN

The current study was designed to investigate whether and to what extent diverse prenatal sensory experience could prevent the quail embryo's perceptual window from narrowing to prefer a species-typical auditory stimulus, the bobwhite maternal call, following hatching. By passively exposing the developing embryo to a variety of audio and audio-visual presentations of calls from different quail species, this study aimed to explore whether and to what extent this modified experience can interfere with the emergence of a seemingly innate species-specific auditory preference, at least temporarily. Additionally, the duration of the predicted widened perceptual window was examined using a cross-sectional design, testing chicks over the first week post-hatch, as they amassed increasing amounts of exposure with their conspecific broodmates and the auditory and multisensory stimulation they provide.

Figure 2

Model of Prenatal Perceptual Narrowing



Hypotheses

Experiment 1 focused on whether varied unimodal auditory stimulation presented prenatally around the onset of auditory function facilitates or interferes with the development of a postnatal species-typical auditory preference. By exposing quail embryos to the calls of several different quail species over the course of prenatal development, it was predicted that this experience would keep the perceptual window from narrowing or honing in on the species-typical bobwhite maternal call over the other quail calls presented. While previous research has demonstrated that passive prenatal auditory exposure can increase postnatal malleability (Harshaw & Lickliter, 2010), the use of multiple species calls is unique in the current study.

Hypothesis 1: Bobwhite quail embryos receiving exposure to a species typical call (bobwhite maternal assembly call) prenatally will demonstrate a preference for that specific call at both 24 and 48 hours following hatching.

Hypothesis 2: Bobwhite quail embryos receiving exposure to a species atypical call (Japanese quail maternal assembly call) will demonstrate a preference for that species atypical call at 24 hours following hatching. Previous research has demonstrated that passive exposure to a species-atypical call can alter postnatal preferences. However, without maintenance through postnatal training, this effect is short lived (Harshaw & Lickliter, 2010)

Hypothesis 3: Bobwhite quail embryos exposed to a soundtrack of maternal calls from several different species of quail (Northern bobwhite quail, Japanese quail, scaled quail; “Quail Mix”) will not demonstrate a preference for any quail maternal call (of those previously presented) at 24 hours following hatching. Previous studies of bilingual

human infants suggest that increased auditory variation through passive exposure results in a lack of preference between the languages the infant was exposed to prenatally (Byers-Heinlein, Burns, & Werker, 2010).

Hypothesis 4: Quail chicks exposed to the “Quail Mix” prenatally will, after accruing experience with their broodmates postnatally, develop a species typical auditory preference for the bobwhite maternal assembly call by 48 hours following hatching. Without maintenance of the broadened perceptual window through auditory enrichment following hatching, quail chicks, like other precocial birds, will rapidly acquire a species-typical preference through stimulation from the self and conspecific broodmates (Gottlieb, 1971, 1978, 1984; Gottlieb & Vandenberg, 1968).

Table 1

Experiment 1 Hypotheses

| Condition | Stimulation | Expected Preference 24hr | Expected Preference 48hr |
|----------------|---------------|--------------------------|--------------------------|
| Bobwhite | Auditory only | Bobwhite | Bobwhite |
| Japanese Quail | Auditory only | Japanese Quail | Japanese Quail |
| “Quail Mix” | Auditory only | None | Bobwhite |
| Control | None | Bobwhite | Bobwhite |

*Quail chicks tested between Bobwhite vs. Japanese Quail Calls

Experiment 2 investigated whether prenatal auditory enrichment could generalize to include stimuli that were not originally presented prenatally. Prenatal auditory enrichment has been shown to effect the underlying auditory neural architecture (Alladi, Roy, Singh, & Wadhwa, 2005A, 2005B; Chaudhury & Wadhwa, 2009; Wadhwa, Anand, & Bhowmick, 1998), decrease emotional reactivity (Kim et al., 2006), and improve performance in auditory discrimination tasks (Xu, Yu, Cai, Zhang, & Sun, 2009). Therefore, I predicted that the perceptual narrowing window would remain open not only to the specific auditory stimuli that the chick was originally exposed to, but would also remain open to a novel call.

Hypothesis 1: Bobwhite quail embryos exposed to a soundtrack of maternal calls from several different species of quail (Northern bobwhite quail, Japanese quail, scaled quail; “Quail Mix”) will not demonstrate a preference for a familiar (bobwhite quail) or novel call (California quail) at 24 hours following hatching.

Hypothesis 2: Quail chicks originally exposed to the “Quail Mix” prenatally will, after accruing ongoing experience with their broodmates postnatally, develop a species typical auditory preference for the bobwhite maternal assembly call over the novel California quail call by 48 hours following hatching. Similar to Experiment 1, without postnatal auditory enrichment to keep the perceptual narrowing window open to these alternative calls, a species-typical preference will arise with exposure to conspecific and self-stimulation in the rearing environment following hatch (Gottlieb, 1971, 1978, 1984; Gottlieb & Vandenberg, 1968).

Table 2

Experiment 2 Hypotheses

| Condition | Stimulation | Expected Preference 24hr | Expected Preference 48hr |
|-------------|---------------|--------------------------|--------------------------|
| “Quail Mix” | Auditory only | None | Bobwhite |
| Control | None | Bobwhite | Bobwhite |

*Quail chicks tested between Bobwhite vs. California (novel) Quail Calls

Experiment 3 investigated whether bimodal presentation of the mixed quail vocalizations paired with either a synchronous or asynchronous pulsed light, would facilitate or impede perceptual narrowing. While there has been human and comparative evidence that intersensory redundancy facilitates learning and memory, it does so for certain features or properties of the stimulation (Bahrick & Lickliter, 2000; Lickliter, Bahrick, & Honeycutt, 2004; Vaillant, Bahrick, & Lickliter, 2009; Vaillant, 2012). There have been no previous studies investigating whether perceptual narrowing is supported primarily through the narrowing of the discrimination of amodal (facilitated by multimodal stimulation) or modality-specific (facilitated by unimodal stimulation) properties of stimulation. It has been suggested that because of the multimodal nature of communication and the simultaneous narrowing of multiple sensory systems, that perceptual narrowing occurs for the amodal properties of stimulation (Pascalis, Loevenbruck, Quinn, Kandel, Tanaka, & Lee, 2014). However, previous research on different species of precocial birds has provided conflicting evidence as to whether species-typical auditory preferences are directed by tempo, rhythm, pitch, frequency modulation, or some combination thereof (Gottlieb 1978, 1980).

Hypothesis 1: Bimodal synchronous stimulation will facilitate learning of the amodal properties (tempo, intensity, rhythmic pattern) of the Quail Mix audio. If perceptual narrowing is supported primarily by sensitivity to amodal properties, then quail embryos receiving the bimodal synchronous presentation of the Quail Mix should demonstrate enhanced learning and memory of all calls found in the auditory enrichment, and not show a preference for any of the calls at 24 hours following hatching. Similar to bilingual newborns with a rich history of synchronous auditory/vestibular exposure to multiple languages (Byers-Heinlein, Burns, & Werker, 2010), these quail chicks should not have a significant preference for any of the calls presented prenatally.

Hypothesis 2: If prenatal perceptual narrowing occurs primarily through the discrimination of the amodal properties of stimulation, then bimodal synchronous stimulation will facilitate learning and memory for these properties above and beyond unimodal auditory exposure. Therefore, quail chicks receiving this redundant stimulation prenatally will remain without a preference for the species-typical call at 48 hours following hatching, an additional 24 hours compared to unimodal conditions.

Table 3

Experiment 3 Hypotheses

| Condition | Stimulation | Expected Preference 24hr | Expected Preference 48hr |
|------------------|------------------------------|---------------------------------|---------------------------------|
| “Quail Mix” | Auditory only | None | Bobwhite |
| “Quail Mix” | Asynchronous Auditory/Visual | None | Bobwhite |
| “Quail Mix” | Synchronous Auditory/Visual | None | None |
| Control | None | Bobwhite | Bobwhite |

*Quail chicks tested between Bobwhite vs. Japanese Quail Calls

CHAPTER IV

GENERAL METHOD

Subjects

Subjects were 555 incubator reared bobwhite quail chicks (*Colinus virginianus*). Fertilized unincubated eggs were received weekly from a commercial supplier and set in an incubator maintained at 75-80% relative humidity and 37.5°C. Embryonic age was calculated on the basis of the first day of incubation as Day 0, and so forth. At Day 15 of 23 days of incubation, eggs were separated and transferred from the common incubator into a smaller, Styrofoam portable incubator. Following hatching, groups of 12-15 subjects were housed together in a rearing tub inside of a larger laboratory common rearing room, which houses approximately 200 bobwhite quail chicks in separate group bins, until testing. Chicks were provided constant access to food and water, except during testing sessions. Ambient air temperature was maintained at approximately 30° C both in the rearing and testing rooms. After testing, chicks were given physical enrichment in the form of a small colored translucent plastic igloo that provided visual stimulation and hiding opportunities.

Stimuli

Auditory Stimuli

The auditory stimuli used in the study consisted of maternal assembly calls from a variety of quail species. The northern bobwhite maternal assembly call consists of five notes, lasting 3s in total, and has dominant frequencies of 1.2–1.5 and 2–2.4 kHz. The Japanese quail maternal assembly call consists of five notes, but is 1.8s long, and has

dominant frequencies of .75–.85 and 1.6–1.7 kHz. Both the bobwhite and Japanese quail calls were cleaned courtesy of the The Borror Laboratory of Bioacoustics (Columbus, OH). The scaled quail maternal assembly call is approximately .9s long and consists of two notes with a dominant frequency of 1.9-2.4 kHz. Lastly, the California quail maternal assembly call consists of three notes, approximately .85s in duration, with dominant frequencies of .9-1.5 and 3.7-4.7 kHz. The scaled quail and California quail calls were courtesy of the Cornell Ornithological Acoustic Lab. All audio stimuli were examined for duration and dominant frequencies using *Raven Lite 1.0* bioacoustics research program from the Cornell Lab of Ornithology. Waveforms and Spectrograms of the auditory stimuli are visualized in Figure 3 and Figure 4.

Figure 3

Waveforms of the Auditory Stimuli

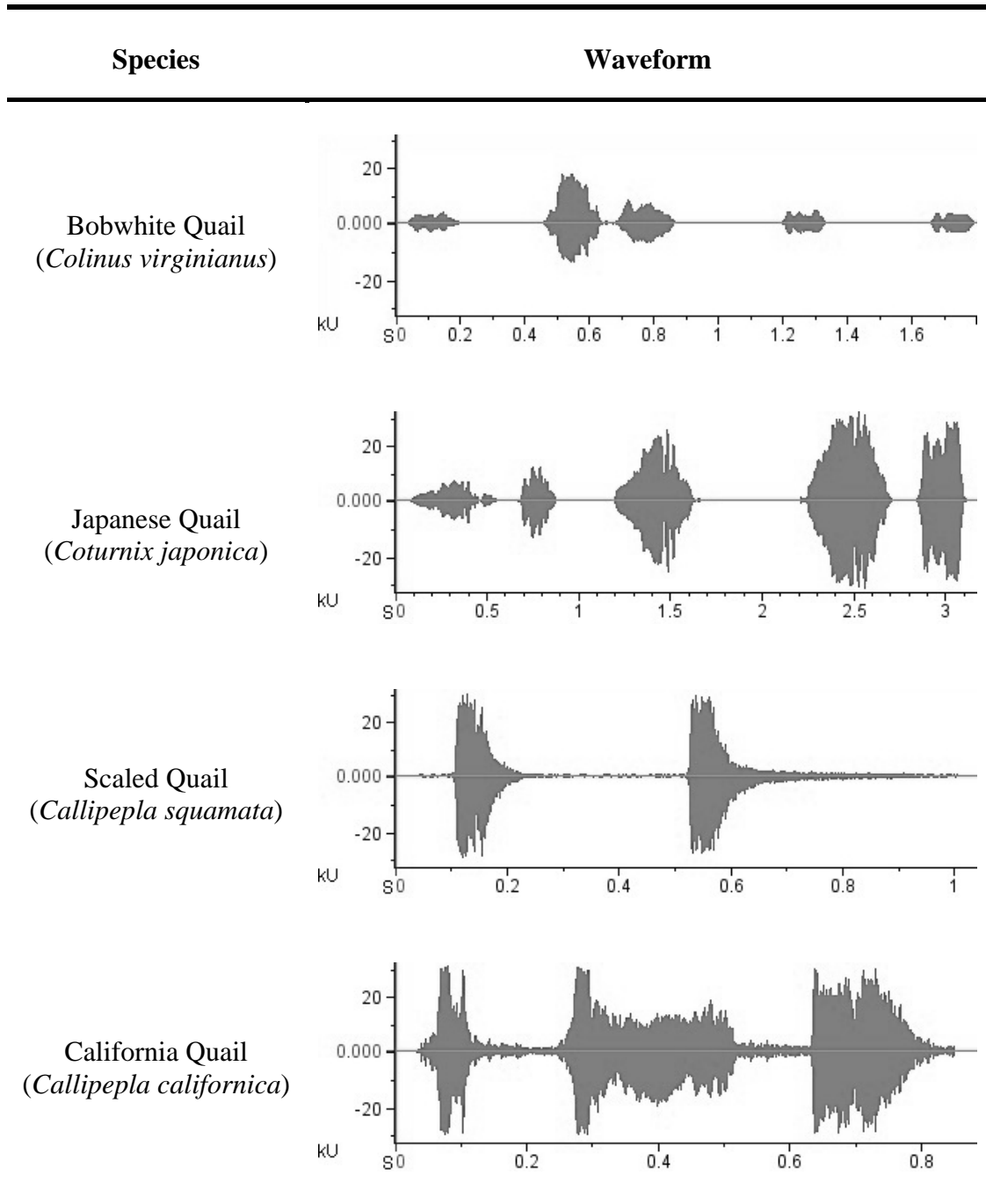
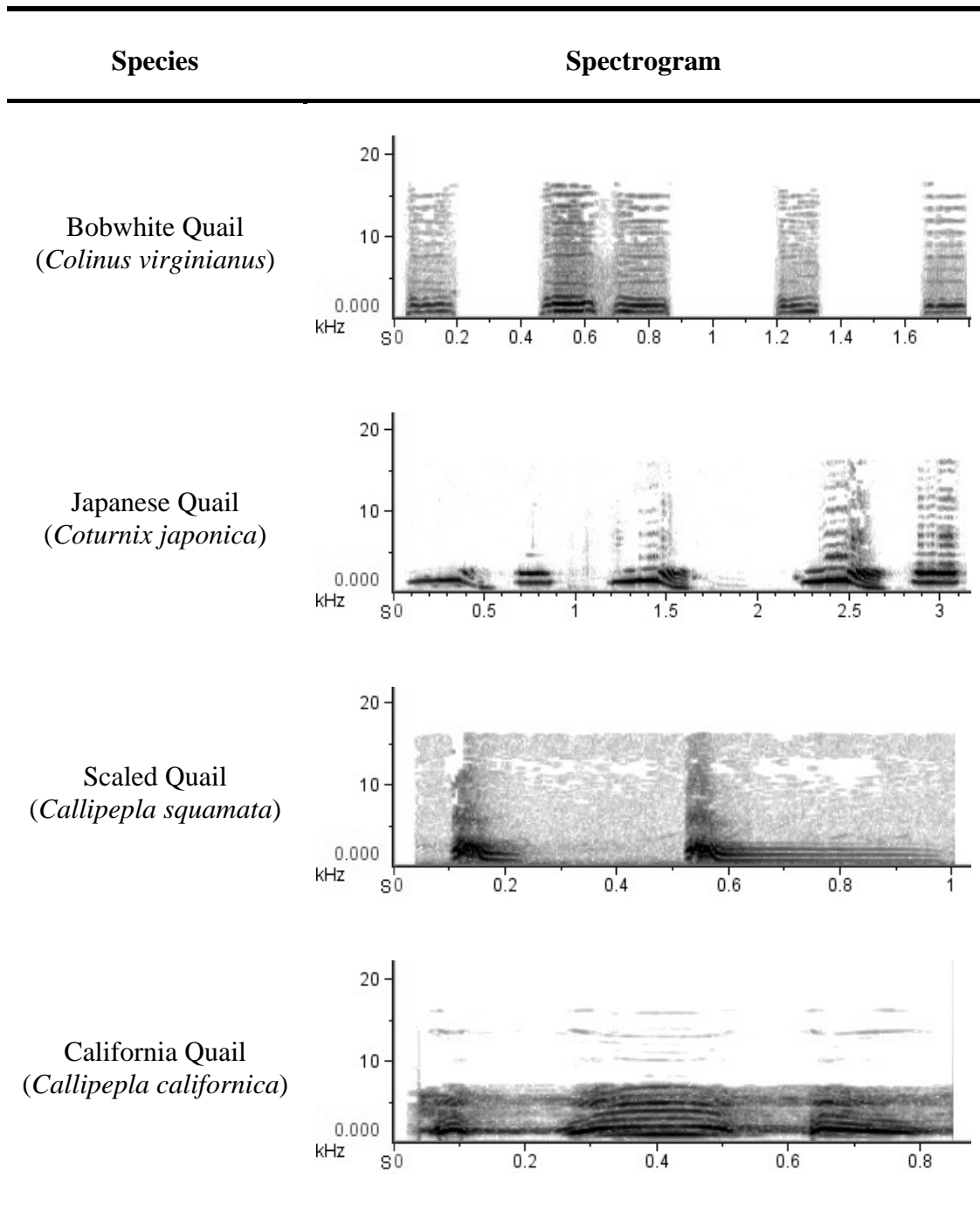


Figure 4

Spectrograms of the Auditory Stimuli



The “Quail Mix” auditory stimulation consisted of the bobwhite, Japanese, and scaled quail calls sequentially in varying order. A call would play for approximately 20 seconds with a minimum of 4 repetitions of the full call before switching to a different species. The duration in between different calls varied between .5-2s depending on and preceding and following recordings. Pauses in between repetitions of the same call also varied, between .5s between iterations in the scaled quail recording, 1.5 between calls in the Japanese quail recording, and 3s between calls in the bobwhite recording. These pauses between repetitions were not manipulated and reflect the natural tempo and frequency of the specimen at the time of recording.

Bimodal Audiovisual Stimuli

Bimodal audiovisual presentation consisted of the Quail Mix auditory enrichment paired with a pulsed light. The light was delivered by a 40 watt incandescent bulb located above the incubator. This provided approximately 450 lumens of light through two large clear plastic windows on top of the incubator. Synchronous bimodal audiovisual stimulation consisted of the light pulsed in synchrony with the notes of each call. Asynchronous bimodal audiovisual stimulation consisted of the light being delayed from the onset of the auditory presentation by 300ms by way of a digital delay. The 300ms offset was used as previous paradigms have successfully used this delay to create sufficient asynchrony. Additionally, the 300ms offset was shorter than the latency between the individual notes of each call and the latency between call shifts in the Quail Mix audio, therefore no unintentional synchrony occurred.

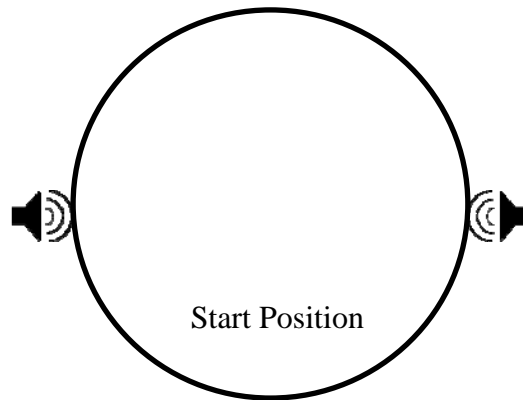
Apparatus

Audio and audio-visual stimulus presentations were delivered by means of a computer with a custom designed software program connected by way of an amplifier, digital delay, and digital/analog converter box to a speaker and small desk lamp. Using this program, stimulation was presented either audio-only, synchronous audio-visual, or asynchronous audio-visual. Multimodal (audio-visual) presentation consisted of a pulsing light paired with the individual notes of each call. The speaker was placed on the top of the portable incubator, facing downward toward the eggs, and was calibrated not to exceed 60db. Similarly, for audio-visual presentations, the 40watt lamp was placed facing the clear plastic window on top of the portable incubator.

Behavioral tests were conducted with chicks at either 24 or 48 hours of age in an arena 130 cm in diameter, encircled by a curtained wall 60 cm in height. The arena surface is painted white with an opaque white cover around the wall of the arena, all within a uniformly curtained room in order to prevent chicks from using any external landmarks to direct their behavior in the arena. A video camera mounted directly above the arena allowed for remote observation and data collection. Two semi-circular approach areas each comprising approximately 5% of the total area of the testing arena were designated using an animal tracking software program, Noldus Ethovision (see Figure 5). Both approach areas contain a small externally mounted speaker which allows for presentation of the auditory stimuli during testing trials. The volume of each call was calibrated to 60DB.

Figure 5

Diagram of the Behavioral Testing Arena



Approach areas on either side of the arena broadcast either the species-typical bobwhite quail maternal call or a species-atypical maternal call.

Procedure

Bobwhite quail chicks were divided into 6 experimental conditions: (1) a Unimodal Quail Mix group, which received auditory exposure to maternal assembly calls from three species of quail (bobwhite (*Colinus virginianus*), Japanese (*Coturnix japonica*), and scaled quail (*Callipepla squamata*)), (2) a Bimodal Synchronous Quail Mix group which received the mixed species audio soundtrack with a pulsed light synchronized to the individual notes of each call, (3) a Bimodal Asynchorous Quail Mix group, which received the mixed species audio soundtrack with a pulsed light offset from the call bursts by 300ms (4) a Unimodal Bobwhite group, which received auditory exposure to only a bobwhite maternal assembly call, (5) a Unimodal Japanese quail group, which received auditory exposure to only a Japanese quail call, and (6) a Control group, which received no modified prenatal stimulation.

All experiments in the current project used a cross-sectional design in which approximately 60 chicks per condition were divided into 24 hr and 48 hr testing groups in order to assess the trajectory of perceptual narrowing over early postnatal development. Eggs that received altered prenatal stimulation did so starting on Day 15 of incubation. While the onset of auditory function in bobwhite quail embryos is not known, estimations were made on the basis of previous research with domestic chickens on prenatal cochlear activation (Saunders, Coles, & Gates, 1973). Stimulation was on a schedule of 10 min/hr for 24 hours per day from Day 15 until hatch. Although the typical incubation duration for bobwhite quail embryos is 23 days, the majority of subjects hatched on day 24. Late hatching occurred across all conditions, most likely as the result of being incubated in a less efficient Styrofoam incubator. The postnatal rearing environment consisted of a clear standard laboratory bin of approximately 12 chicks, where no further experimental stimulation occurred. Chicks had constant access to food and water except during testing trials. Chicks had direct contact with their own vocalizations, their broodmates in the same bin, as well as auditory and olfactory stimulation from approximately 150 other bobwhite quail chicks housed in the rearing room.

Testing was conducted at either 24 or 48 hours postnatally. Each chick was tested individually and was only tested once. The testing consisted of a 5 minute (300s) simultaneous choice task between the species typical bobwhite maternal call and either a non-conspecific Japanese quail call (included in the Quail Mix) or the non-conspecific California quail call (not included in the Quail Mix). Preference for a call was determined by the proportion of time spent in the approach with the speaker broadcasting that call over total time spent in both approach areas (Proportion of Total Duration or PTD score).

Table 4

Total Subjects by Condition and Age of Testing

| Prenatal Condition | Postnatal Test | 24 Hours | 48 Hours | Total |
|----------------------------------|-----------------------|-----------------|-----------------|--------------|
| Experiment 1 | | | | |
| Quail Mix (Audio Only) | BW vs. JQ | 32 (1) | 30 (0) | |
| Bobwhite Audio | BW vs. JQ | 30 (0) | 35 (1) | |
| Japanese Quail Audio | BW vs. JQ | 30 (1) | 30 (2) | |
| Control (no manipulated stimuli) | BW vs. JQ | 33 (3) | 33 (3) | |
| Experiment 2 | | | | |
| Quail Mix (Audio Only) | BW vs. California | 35 (5) | 39 (9) | |
| Control (no manipulated stimuli) | BW vs. California | 32 (4) | 30 (5) | |
| Experiment 3 | | | | |
| Bimodal Synchronous Quail Mix | BW vs. JQ | 31 (0) | 36 (5) | |
| Bimodal Asynchronous Quail Mix | BW vs. JQ | 33 (0) | 62 (2) | |
| Total | | | | 555 |

Note: Non Responders represented in parentheses were not used in final data analysis

Data Analyses

Chicks that did not enter either approach area during testing were considered Non Responders and were excluded from final data analysis. These individuals failed to move a significant distance (<10cm) during the 300s trial, typically falling asleep during the testing trial. A Chi-square test was used to determine if any one condition or time point had significantly more Non Responders. The Chi-square tests indicated that there were no significant differences between groups or time points on the number of Non Responders: $X^2 (7, N = 555) = 7.19, p = .410$.

For the remaining subjects, a proportion of total duration (PTD) score was calculated based on the time a chick spent in the approach area presenting the species typical call relative to the total time spent in both species-typical and species-atypical

approach areas. Therefore, a PDT score of .5 represented chance responding, a score over .5 corresponds to a species-typical preference, and a score under .5 represents a non-conspecific preference. One-sample t-tests were used to determine whether the PDT scores from a particular condition at a single time point was significantly different from chance. Significance levels <.05 (two-tailed) were used to evaluate results from the t-tests. To compare conditions between each other at each testing age, a One-Way Analysis of Variance (ANOVA) with post-hoc Bonferroni multiple comparison tests was used with the PTD scores.

PTD Formula:

$$\text{PTD} = \frac{\text{Time Spent in Conspecific Call Area}}{\text{Total Time Spent in Both Call Areas}}$$

CHAPTER V

EXPERIMENT 1

Unimodal Perceptual Narrowing (Preventing Narrowing through Prenatal Auditory Enrichment)

Previous work in humans has demonstrated that perceptual narrowing of linguistic features, such as prosody, can occur prenatally (Byers-Heinlein, Burns, & Werker, 2010; DeCasper et al., 1994; Krueger et al., 2004; Nazzi, Bertoncini, & Mehler, 1998). Additionally, perceptual narrowing of phonemes has been shown to rapidly occur during early postnatal development, with some experiments indicating that auditory enrichment to non-native phonemes can, at least temporarily, keep the perceptual window “open” to distinguishing those sounds (Kuhl et al., 2003). This experiment manipulated prenatal auditory stimulation in bobwhite quail embryos from the onset of auditory function to assess whether it is possible to keep the perceptual narrowing window open and effectively interfere with the emergence of a species typical auditory preference postnatally. Classic and contemporary work with precocial birds has demonstrated a robust effect of unimodal auditory and bimodal auditory/visual or auditory/vestibular stimulation on facilitating learning and memory for a species typical maternal call (Lickliter, Bahrack, & Honeycutt, 2004; Lickliter & Hellwell, 1992; Honeycutt & Lickliter, 2001; Vaillant, Bahrack, & Lickliter, 2009). However, these methods have yet to be applied to perceptual narrowing. This first experiment investigated whether prenatal exposure to unimodal auditory stimulation, either species-typical, species a-typical, or species-mixed would alter postnatal species-typical auditory preferences.

Method

Two hundred and fifty seven bobwhite quail chicks were assigned to one of four conditions: Standard Control, Bobwhite Audio, Japanese Quail Audio, and Quail Mix Audio. Chicks that received stimulation were exposed as embryos (in ovo) to an audio soundtrack starting on day 15 of incubation. Embryos were transferred from a large laboratory incubator into a smaller portable incubator with a turning mechanism situated inside a sound attenuated room. The embryos received their assigned stimulation regime for 10 min each hour for the remainder of incubation. Upon hatch, experimental stimulation was stopped. Each condition was divided into a 24 hr and 48 hr testing group, creating a cross-sectional design (see Table 2). All chicks were tested individually in a simultaneous choice test between the bobwhite and Japanese quail maternal assembly calls, both of which were part of the Quail Mix track.

Results

Comparisons in the proportion of total duration (PTD) chicks from the four groups (Audio Quail Mix (Unimodal), Bobwhite, Japanese, and Control) spent in proximity to the species-typical bobwhite call versus the species-atypical Japanese quail call were conducted using a One-way Analysis of Variance (ANOVA) groups at each time point (24hr, 48hr). At 24 hours there was a significant difference in the proportion of time chicks spent in proximity to the species-typical call versus the species-atypical call, $F(3, 117) = 28.166, p < .001$. Planned comparisons were conducted comparing the PTD scores of the Quail Mix condition to the Bobwhite and Control conditions; similarly the Japanese condition was compared to the Bobwhite and Control conditions. The Quail Mix ($M = .4857, SD = .1962$) group spent a significantly different proportion of time in

proximity to the bobwhite and Japanese quail calls compared to the Bobwhite ($M = .8405$, $SD = .1847$) and Control ($M = .7646$, $SD = .1750$) conditions ($t(117) = -6.635$, $p < .01$). The Japanese ($M = .4121$, $SD = .2890$) condition was also spent a significantly smaller proportion of time in proximity to the species-typical call compared to the Bobwhite and Control groups ($t(117) = -8.087$, $p < .01$). Both the Bobwhite and Control groups spent significantly more time in proximity to the bobwhite maternal assembly call at 24 hours. Given prior results with bobwhite quail, it is not surprising that both the Bobwhite and Control conditions preferred the species-typical bobwhite maternal assembly call. While birds in the Bobwhite condition received experimentally augmented species-typical auditory stimulation, birds in the Control condition were still able to hear their own vocalizations and those of their broodmates without any additional auditory stimulation.

To determine the individual preferences of each group, one-sample t-tests were run comparing the mean Proportion of Total Duration (PTD) score of each group against a value representing chance, .5 or 50%. At 24 hours, Control chicks spent significantly more time in proximity to the bobwhite call, $t(29) = 8.283$, $p < .001$, as did the chicks from the Bobwhite condition, $t(29) = 10.096$, $p < .001$. In contrast, the Audio Mix chicks did not have a significant preference for either call at 24 hours, spending approximately equal time in proximity to both the bobwhite and Japanese quail calls, $t(30) = -.407$, $p = .687$). Chicks from the Japanese quail call condition were spending slightly more time near the Japanese quail call during testing, but this trend did not reach significance with the two-tailed test, $t(29) = -1.666$, $p = .107$). Taken together, the results from 24 hr testing support the hypothesis that chicks given diverse, but ecologically relevant prenatal auditory enrichment do not demonstrate a species-typical auditory preference

At 48 hr testing, all four conditions had a significant preference for the bobwhite maternal assembly call, indicating rapid postnatal narrowing of the perceptual window. The Bobwhite and Control conditions maintained their preference for the bobwhite maternal call, whereas the Audio Mix and Japanese conditions recovered from their prenatal exposure and spent significantly more time close to the bobwhite maternal assembly call. A one-way ANOVA indicated no significant differences between the groups on their mean Proportion of Total Duration scores, $F(3, 121) = 3.918, p = .10$. The Bobwhite ($t(34) = 9.896, p < .001$), Control ($t(29) = 12.318, p < .001$), Japanese ($t(29) = 5.592, p < .001$), and Audio Mix ($t(29) = 5.347, p < .001$) conditions all had a mean PTD score significantly higher than chance (.5) indicating that chicks spent significantly more time near the species-typical bobwhite call compared to the alternative Japanese quail call. The preferences for these groups are shown in Figure 6.

Table 5

Means and Standard Deviations of the PTD Scores for Experiment 1

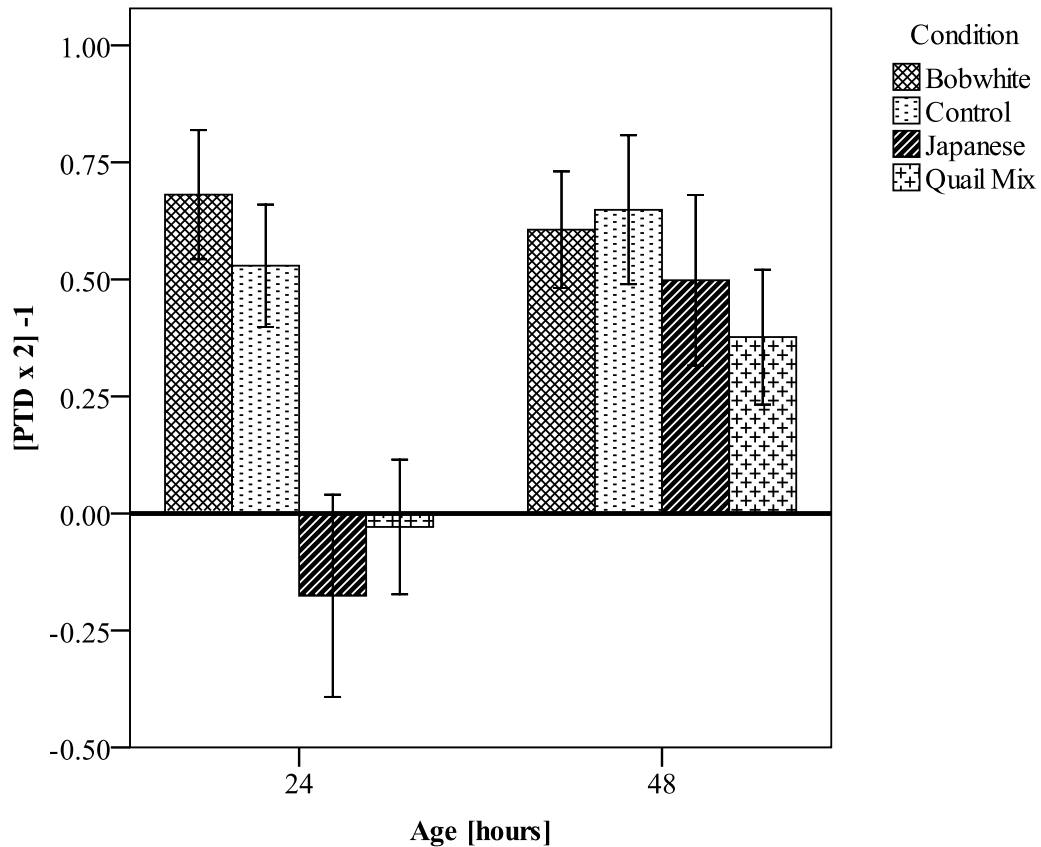
| Condition | Postnatal Test | 24hr | 48hr |
|-----------------|----------------|-----------------------|-----------------------|
| Audio Quail Mix | BW vs. JQ | .48 (.19) N = 31 | .68** (.19) N = 30 |
| Bobwhite | BW vs. JQ | .84** (.18) N = 30 | .80** (.18) N = 35 |
| Japanese Quail | BW vs. JQ | .41 (.28) N = 30 | .74** (.24) N = 30 |
| Control | BW vs. JQ | .76** (.17) N = 30 | .85** (.15) N = 30 |

* Indicates significant preference for the Japanese quail call

**Indicates significant preference for the bobwhite quail call

Figure 6

Proportion of Total Duration Scores Compared to Chance for Experiment 1



Error bars: 95% CI

†Scores intersecting zero indicate no preference for either call.
Scores above zero indicate a preference for the species-typical call.
Scores under zero indicate a preference for the species-atypical call

Discussion

The results of Experiment 1 demonstrate that prolonged passive auditory enrichment during prenatal development can affect postnatal species-typical preferences. In accordance with my hypotheses, chicks that received the Audio Quail Mix prenatally did not have a significant preference for either call, bobwhite or Japanese, that they experienced prenatally; chicks spent approximately equal time in proximity to both calls

during testing at 24 hours following hatch. Whereas birds given enhanced species-typical auditory stimulation or those simply allowed a quiet rearing environment with their own vocalizations and those of their clutch behaved as predicted, showing a preference for their species-typical maternal call. The effect of same-age peers and self-stimulation on postnatal auditory preferences of an adult maternal call in precocial bird species has been previously established (Gottlieb, 1971, 1978, 1984; Gottlieb & Vandenberg, 1968). Lastly, chicks exposed to only one alternative species atypical call prenatally showed a trend towards preferring that atypical maternal call at 24 hours. These effects, while impressive, were short lived.

The effects of prenatal auditory enrichment were temporary, as the chicks rapidly came to prefer their species-typical call in a postnatal environment void of the same consistent presentation of the alternative calls. This is similar to human infants learning a different language – without consistent and ongoing exposure, their perceptual window quickly closes and the infant loses the ability to make those nuanced non-native distinctions (Kuhl, Tsao, & Liu, 2003). Not only is the chick's postnatal environment not reinforcing the calls present in the Audio Quail Mix, it is also rich in species typical stimulation. Chicks are able hear themselves and hear, see, and smell the 12-15 broodmates in their bin and hear the approximately 150 bobwhite quail chicks housed in the same room.

It is possible that postnatal exposure could be used to prolong the effects of prenatal enrichment on perceptual narrowing. This could be as simple as extending the same schedule of passive auditory enrichment to 24 or 48 hours postnatally or providing a brief reminder of the various calls following hatching. Alternatively, a small amount of

contingent exposure to the species-atypical calls postnatally may be a powerful delivery method. Previous research has demonstrated that chicks are able to learn a maternal call variant via contingent presentation in 1/100th of the time of passive exposure (Harshaw, Tourgeman, & Lickliter, 2008). Another way of providing species atypical enrichment postnatally would be to rear bobwhite quail chicks with chicks from other quail species. This would provide not only auditory enrichment, but also rich social experience including auditory and visual redundancy and social contingencies from same-age peers.

While the prenatal auditory enrichment provided in this experiment was able to temporarily interfere the formation of a preference between a species-typical and species-atypical maternal call, this experiment only tested chicks between two calls that were in the original prenatal presentation. How could prenatal auditory enrichment and the alteration of the perceptual narrowing window affect the chick's response to a novel call in the postnatal environment? The following experiment was designed to address to what extent a broad perceptual window generalizes to a novel auditory stimulus.

CHAPTER VI

EXPERIMENT 2

Response to Novelty following Prenatal Auditory Enrichment

Enriched rearing paradigms have demonstrated improvements in learning and memory, a reduction in emotional reactivity, and an increase in exploratory behavior when young organisms are faced with novel stimuli (Baroncelli et al., 2010; Cymerblit-Sabbaa et al., 2013). Early in development the presence of a variety of ecologically valid socially-derived auditory stimuli has been shown to positively affect perceptual narrowing and future language development in humans. Not only does that exposure prime the infant to learn the languages presented, this enrichment alters their sensitivity to languages outside of that original range (Byers-Heinlein & Fennel, 2013). Conversely, the abundant presence of ecologically invalid auditory stimuli, such as the electronic beeps of the machines found in the NICU environment, can have negative effects on language development in preterm human infants (Rand & Lahav, 2014). Further, in domestic chickens, the use of sitar music (ecologically invalid stimulation) as prenatal auditory enrichment has been shown to alter neurobiology associated with learning and memory (Alladi, Roy, Singh, & Wadhwa, 2005A; Chaudhury & Wadhwa, 2009); however during postnatal testing these enriched chicks demonstrated a preference for their species-typical call, no different from control chicks. Experiment 2 addressed how prenatal auditory enrichment, in the form of diverse and ecologically valid auditory stimulation would effect quail chicks' postnatal response to novelty. Specifically, Experiment 2 assessed whether prenatal auditory enrichment can affect sensitivity to and preference for species-specific stimuli, as well as to novel auditory stimuli.

Method

One hundred and thirty-six bobwhite quail chicks were divided into two (2) conditions (Audio Quail Mix, Control) across two (2) time points (24hr, 48hr). Chicks in the Audio Quail Mix group were exposed as embryos (in ovo) to an auditory soundtrack starting on day 15 of incubation, as in Experiment 1. This enrichment consisted of three different calls of quail species (bobwhite, Japanese, and scaled quail) for 10 min each hour for the remainder of incubation. All embryos were transferred from a large laboratory incubator into a smaller portable incubator with a turning mechanism situated inside a sound attenuated room. Following hatching, all groups were tested individually in a simultaneous choice test between the bobwhite call and a California (*Callipepla californica*) quail call. The California quail call served as a novel auditory stimulus.

Results

Results are shown in Table 6. One-sample t-tests were conducted on the Proportion of Total Duration (PTD) score compared to a value of .50 representing chance to determine the postnatal preference of each experimental condition. At 24 hours, chicks that received the Audio Quail Mix prenatally spent significantly more time in proximity to the novel California quail call over the bobwhite quail call, $t(29) = -7.481, p < .001$. In contrast, at 24hr Control chicks spent significantly more time near their species typical bobwhite call, $t(27) = 2.527, p = .018$. The mean PTD scores are shown in Table 6. At 48 hours, chicks in the Audio Quail Mix condition recovered and showed a significant preference for the bobwhite maternal call, $t(29) = 2.180, p = .038$. The Control group continued to prefer their species typical call at 48 hours, $t(24) = 3.276, p = .003$. Results are shown in Table 6.

Independent samples t-tests were conducted to compare the preferences of each group individually at 24 and 48 hours. At 24 hours, there was a significant difference between the Audio Quail Mix and Control Group in their Proportion of Total Duration (PTD) scores, $t(56) = 6.074, p < .001$; Audio Quail Mix chicks preferred the novel California quail call and Control chicks preferred the species-typical bobwhite quail call. However, at 48 hours there was no significant difference between the Audio Quail Mix and Control groups on their PTD scores, $t(53) = .363, p = .718$; both groups spent the majority of their time during testing close to the species-typical bobwhite maternal assembly call over the novel California quail call.

Table 6

Means and Standard Deviations of the PTD Scores for Experiment 2

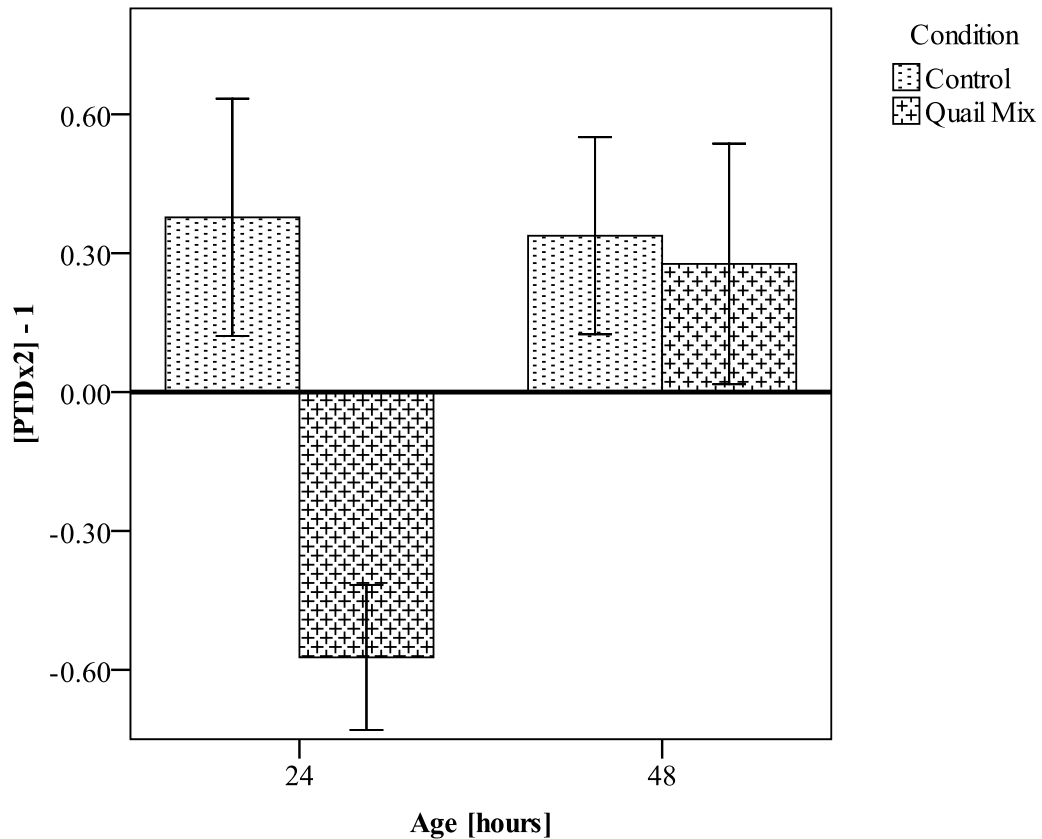
| Condition | Postnatal Test | 24hr | 48hr |
|-----------------|-------------------|-----------------------|-----------------------|
| Audio Quail Mix | BW vs. California | .21* (.20) N = 30 | .63** (.34) N = 30 |
| Control | BW vs. California | .66** (.34) N = 28 | .66** (.25) N = 25 |

* Indicates significant preference for the California quail call

**Indicates significant preference for the bobwhite quail call

Figure 7

Proportion of Total Duration Scores Compared to Chance for Experiment 2



Error bars: 95% CI

† Scores intersecting zero indicate no preference for either call.
Scores above zero indicate a preference for the species-typical call.
Scores under zero indicate a preference for the species-atypical call

Discussion

As predicted, quail chicks that received ecologically relevant auditory enrichment prenatally were significantly more receptive to novel auditory stimuli following hatching. Chicks that received prenatal auditory enrichment spent more time in close proximity to a novel, acoustically distinct call compared to their species-typical call. This is indicative of openness to new experiences and reduced fear of novelty, a representative

consequence of early environmental enrichment (Baroncelli et al., 2010; Cymerblit-Sabbaa et al., 2013). In the context of perceptual narrowing, the prolonged prenatal auditory enrichment interfered with the quail chicks honing in on their species-specific maternal call. Not only did this result in a lack of preference between the calls used in the original exposure (i.e. native stimuli) seen in Experiment 1, but this effect generalized to a novel stimulus. In Experiment 2, the California quail call was chosen since, while it is distinct in tempo and pitch from the other three calls the embryos were exposed to, it was still a species of North American quail. It would be interesting to assess how wide or limiting the perceptual narrowing window is by using stimuli outside of the *Galliformes* order, including other bird species or even artificial or mechanical sounds.

In both Experiment 1 and Experiment 2, the effect of prenatal auditory enrichment on perceptual narrowing was temporary, with chicks quickly recovering from their early enrichment. Between 24 hours and 48 hours after hatching, the effect of prenatal auditory exposure rapidly diminished. This specialization or narrowing was anticipated but still impressive considering the long prenatal history of diverse stimulation in the Audio Quail Mix group, approximately 36 hours of passive prenatal exposure distributed over 9 days, from the onset of auditory function. The postnatal rearing environment provided chicks with incredibly salient species-typical stimulation that included multimodal information and social contingency in interactions with broodmates.

Similar to first experiment, chicks received large amount of species-typical experience postnatally while simultaneously being deprived of other experiences including other sounds and natural accommodations, given laboratory rearing conditions.

By either extending auditory enrichment into the postnatal environment or restricting postnatal species-typical social exposure, the perceptual narrowing window may be more malleable. The delivery method of the original prenatal exposure might also be altered in order to extend the duration of effect. Experiment 3 addressed whether prenatal auditory enrichment may be more efficient and long-lasting if it consists of redundant bimodal stimulation occurring across auditory and visual modalities, as opposed to unimodal (auditory-only) presentations.

CHAPTER VII

EXPERIMENT 3

Bimodal Facilitation of Perceptual Narrowing

Perceptual narrowing has been shown to occur both for individual sense modalities and for the integration of events using two or more sense modalities. Both unimodal and bimodal redundant prenatal stimulation have been shown to facilitate learning of either modality specific or amodal properties of stimulation, respectively, in bobwhite quail embryos and chicks (Bahrick & Lickliter, 2000; Lickliter, Bahrick, & Honeycutt, 2004; Vaillant, Bahrick, & Lickliter, 2009; Vaillant, 2012). According to the Intersensory Redundancy Hypothesis (IRH), redundant bimodal sensory stimulation facilitates the differentiation, learning, and memory of amodal properties of stimulation, such as rhythm, tempo, and intensity. On the other hand, unimodal stimulus presentation recruits selective attention for the modality specific properties of the stimulus, such as the pitch of auditory stimulation (Bahrick & Lickliter, 2012). Experiment 3 was designed to assess which properties of stimulation, amodal or modality specific, are more effective at influencing early perceptual narrowing. Although it has been suggested that perceptual narrowing occurs for the amodal properties of stimulation due to the socially-derived nature of perceptual narrowing process (Pascalis, et al., 2014), no empirical data currently supports this claim. By comparing the effectiveness of the auditory enrichment regime on its own to one paired with another sense modality (visual), Experiment 3 aimed to determine which properties of stimulation are most effective for supporting prenatal perceptual narrowing.

Method

One-hundred and fifty-five bobwhite quail embryos were divided into two conditions: Bimodal Synchronous Quail Mix and Bimodal Asynchronous Quail Mix. In the Bimodal Synchronous Quail Mix condition, embryos received a pulsed light synchronized to each note of the maternal quail calls. Embryos in the Bimodal Asynchronous condition received a pulsed light offset from the notes of each call by 300ms – this stimulation can be likened to a film with the audio noticeably out-of-synchrony with the visual image. Starting on day 15 of incubation, all embryos were exposed to an auditory soundtrack consisting of a mix of maternal calls from three species of quail: bobwhite, scaled, and Japanese quail. The embryos received their assigned stimulation for 10 min each hour for the remainder of incubation. Upon hatching, chicks were removed from experimental stimulation and reared in groups of 12-15 chicks in a rearing room. Each condition was divided into a 24 hr and a 48 hr testing groups, creating a cross-sectional design. All chicks were tested individually in a simultaneous choice test between bobwhite and Japanese quail maternal assembly calls.

Results

A One-way Analysis of Variance (ANOVA) was used to compare the mean PTD scores of the four (Audio Quail Mix (Unimodal), Bimodal Synchronous Quail Mix, Bimodal Asynchronous Quail Mix, and Control) groups at each time point (24hr, 48hr). At 24 hours following hatching, there was a significant difference between the conditions ($F(3, 121) = 8.780, p < .001$). Post hoc Bonferroni tests found a significant difference between the Control condition ($M = .7646, SD = .1750$) compared to the Audio Quail Mix ($M = .4857, SD = .1962$) and Bimodal Asynchronous Quail Mix ($M = .5036, SD =$

.2848) conditions. Control birds spent significantly more time in close proximity to the species-typical bobwhite maternal call whereas the Audio Quail Mix and Bimodal Asynchronous Quail Mix groups showed no significant preference for either maternal call, spending approximately equal time close to the bobwhite or Japanese calls. Contrary to my hypothesis there was no significant difference in the proportion of time spent in proximity to the species-typical call between Controls ($M = .7646$, $SD = .1750$) and the chicks in the Bimodal Synchronous Quail Mix ($M = .6655$, $SD = .3149$) condition, suggesting that redundant multimodal presentation of the Quail Mix audio was not effective in keeping the perceptual narrowing window open following hatching.

To determine the individual preferences of each group, one-sample t-tests were run comparing the mean Proportion of Total Duration (PTD) score of each group against a value representing chance, .5. At 24 hours, Control birds had a significant preference for the bobwhite call ($t(29) = 8.283$, $p < .001$) as did the Bimodal Synchronous Quail Mix group ($t(30) = 2.962$, $p = .006$). In contrast, chicks from the Audio Quail Mix (Unimodal) condition ($t(30) = -.407$, $p = .687$) and Bimodal Asynchronous condition ($t(32) = .073$, $p = .943$) failed to display a significant preference for either call during postnatal testing, spending approximately equal time in close proximity to each.

At 48 hours, the Control ($t(29) = 12.318$, $p < .001$) and Bimodal Synchronous ($t(30) = 3.748$, $p = .001$) conditions continued to spend a significant portion of the testing trial in proximity to the species-typical bobwhite call. The Audio Quail Mix (Unimodal) group demonstrated a recovery from the initial prenatal enrichment and also displayed a significant preference for the bobwhite call at 48 hours ($t(29) = 5.347$, $p < .001$).

Surprisingly, the Bimodal Asynchronous group did not recover from their prenatal exposure to the Quail Mix audio and asynchronous pulsed light stimulation by 48 hr following hatching. Batch A of the Bimodal Asynchronous Quail Mix group spent the majority of their time during testing in close proximity to the Japanese quail call ($t(31) = -2.159, p = .039$), counter to the species-typical response. This was unexpected and therefore a replication was run to determine if the result was meaningful. Batch B was run several weeks later, received the same prenatal experience as Batch A, and the chicks displayed no significant preference for either the bobwhite or Japanese quail calls ($t(29) = 1.997, p = .056$). Batch A and Batch B for the Bimodal Asynchronous Quail Mix 48 hour condition were then combined and no significant preference was detected ($t(59) = .159, p = .874$). The failure of the Bimodal Asynchronous Quail Mix group to recover from prenatal enrichment is unique among all other conditions in this series of experiments.

At 48 hours, a one-way ANOVA indicated significant differences between the four conditions ($F(3, 147) = 16.984, p < .001$). However, Control ($M = .8519, SD = .1565$), Audio Quail Mix (Unimodal) ($M = .6884, SD = .1930$), and Bimodal Synchronous Quail Mix ($M = .6543, SD = .2279$) groups all spent significantly more time in proximity to the bobwhite maternal assembly call over the Japanese maternal assembly call during testing. However, exactly how strongly they preferred the call was different, as revealed by post hoc Bonferroni contrasts. Above and beyond the other groups, Controls strongly preferred the bobwhite call, spending on average over 80% of their time in proximity to the bobwhite call. There was no significant difference between the Audio Quail Mix (Unimodal) and Bimodal Synchronous groups at 48 hours. Lastly, the

Bimodal Asynchronous ($M = .5051$, $SD = .2570$) group stood out from the other groups, displaying no preference for either call at 48 hours; an additional 24 hours past when all other enriched groups recovered and preferred the species-typical call. Means and standard deviations are summarized in Table 7.

Table 7

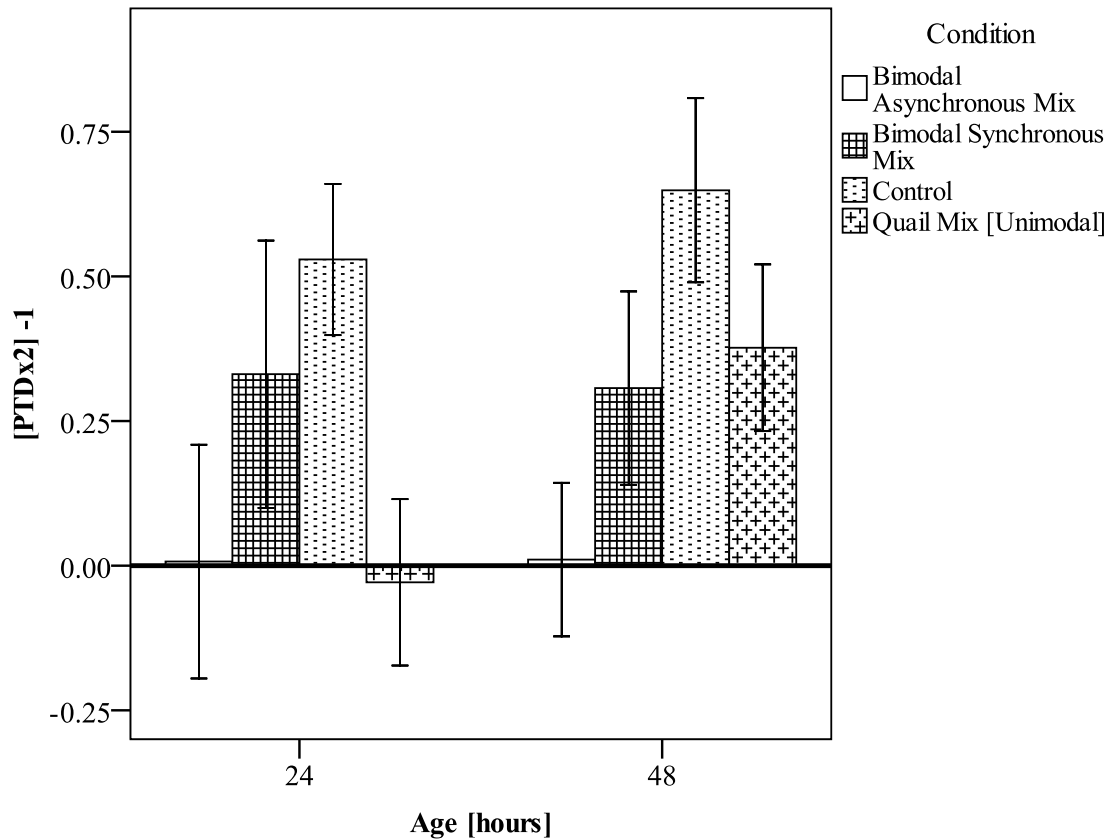
Means and Standard Deviations of the PTD Scores for Experiment 3

| Condition | Postnatal Test | 24hr | 48hr |
|--------------------------------|----------------|----------------------|-----------------------------------|
| Control | BW vs. JQ | .76* (.17) N = 30 | .85* (.15) N = 30 |
| Audio Quail Mix (Unimodal) | BW vs. JQ | .48 (.19) N = 31 | .68* (.19) N = 30 |
| Bimodal Synchronous Quail Mix | BW vs. JQ | .66* (.31) N = 31 | .65* (.22) N = 31 |
| Bimodal Asynchronous Quail Mix | BW vs. JQ | .50 (.28) N = 33 | .50 (.25) N = 60 (combined) |

*Indicates significant preference for the bobwhite quail call

Figure 8

Proportion of Total Duration Scores Compared to Chance for Experiment 3



Error bars: 95% CI

†Scores intersecting zero indicate no preference for either call.
 Scores above zero indicate a preference for the species-typical call.
 Scores under zero indicate a preference for the species-atypical call

Discussion

These findings not only suggest that early auditory perceptual narrowing occurs primarily through the modality specific properties of the calls but also that other factors, such as unusually early light exposure, can affect the perceptual narrowing window and interfere with auditory learning. Contrary to my hypothesis, chicks that received bimodal synchronous presentation of the “Quail Mix” prenatally did not perform differently from

controls, indicating that the presentation of the enrichment was ineffective. While intersensory redundancy would typically facilitate learning and memory, the particular stimulation used in this experiment may have been too intense and therefore counteracted any potential benefits. This is similar to the findings of Radell and Gottlieb (1992) wherein inappropriate or intense multimodal stimulation was ineffective. The bimodal stimulation in the current study could be augmented in future studies to identify a particular sensory milieu could make the prenatal auditory enrichment more effective.

However, the prenatal auditory enrichment did have a more enduring effect when paired with asynchronous pulsed light when compared to those chicks that received either only audio stimulation or audio stimulation paired synchronously with the pulsed light. This implies that the extraneous prenatal light exposure might have prevented chicks from benefitting from auditory experience from their broodmates postnatally, thereby increasing the duration of their wide perceptual window beyond that of the Audio Quail Mix (Unimodal) group. Similarly, the unusually early light exposure experienced by preterm human infants has been shown to interfere with the auditory system (Rand & Lahav, 2014). However, the independent effects of the prenatal auditory enrichment and the unusually early light exposure would need to be assessed in future research in which auditory and visual exposure were more distally temporally separated instead of co-occurring 300ms offset from one another.

Table 8

Summary of the Means and Standard Deviations of the PTD Scores

| Condition | Postnatal Test | 24hr | 48hr |
|---------------------------------------|-------------------|-----------------------|-----------------------------------|
| Bobwhite | BW vs. JQ | .84* (.18) N = 30 | .80* (.18) N = 35 |
| Japanese Quail | BW vs. JQ | .41 (.28) N = 30 | .74* (.24) N = 30 |
| Control | BW vs. JQ | .76* (.17) N = 30 | .85* (.15) N = 30 |
| Control | BW vs. California | .66* (.34) N = 28 | .66* (.25) N = 25 |
| Audio Quail Mix (Unimodal) | BW vs. JQ | .48 (.19) N = 31 | .68* (.19) N = 30 |
| Audio Quail Mix (Unimodal) | BW vs. California | .21** (.20) N = 30 | .63* (.34) N = 30 |
| Bimodal Synchronous Quail Mix | BW vs. JQ | .66* (.31) N = 31 | .65* (.22) N = 31 |
| Bimodal Asynchronous Quail Mix | BW vs. JQ | .50 (.28) N = 33 | .50 (.25) N = 60 (combined) |

*Indicates significant preference for the bobwhite quail call

** Indicates significant preference for the species atypical call

CHAPTER VIII

GENERAL DISCUSSION

The early and seemingly effortless emergence of species-typical perceptual preferences has been shown to be the result of interactions between the organism and the social and ecological stimulation found in its characteristic ontogenetic niche. However, the majority of research on perceptual development has focused on how stimulus exposure promotes positive processes of acquisition and sensitization; the regressive phenomenon of perceptual narrowing has only recently received attention (Lewkowicz, 2014). Along with the existing literature on progressive perceptual developmental mechanisms, the addition of evidence from prenatal sensory enrichment on perceptual narrowing can provide a more complete account of how experience contributes to development (Aslin & Pisoni, 1980).

While longitudinal studies of human infants have demonstrated an association between experience, age, and waning of perceptual discrimination skills, there has been a lack of research on the mechanisms involved in the perceptual narrowing process, particularly during prenatal development. Although theories have been proposed (Pascalis et al., 2014), the current project is the first to explore what kind of sensory stimulation, unimodal or multimodal, and therefore what aspects of stimulation (amodal or modality-specific) are the most efficient at promoting perceptual narrowing and the emergence of species-typical preferences during prenatal development. Knowing to what extent prenatal sensory enrichment can alter the perceptual narrowing window could help inform the care of preterm human infants (Jansson-Verkasalo, et al., 2010; Krueger, Holditch-Davis, Quint, & DeCasper, 2004). By delivering the right kind and amount of

sensory stimulation at the appropriate time, it may be possible to mitigate the deleterious effects of a preterm birth on perceptual, cognitive, and social development as well as future language acquisition.

Experiment 1 investigated whether unimodal prenatal auditory enrichment could interfere with the development of the otherwise robust species-typical preferences found in bobwhite quail neonates. In support of my predictions, quail chicks that received diverse prenatal auditory enrichment in the form of ecologically relevant calls from a variety of species from the same genus (“Quail Mix”) displayed altered patterns of perceptual narrowing. Compared to chicks that received species-typical auditory exposure or chicks that received no manipulated exposure, bobwhite quail chicks that received the Quail Mix did not show a species-typical preference for their species’ call compared to another atypical call originally presented prenatally. Indeed, at 24hr following hatch, these chicks had no significant preference for either call. In humans, this would be akin to infants who coacquire multiple first languages, in-utero. Byers-Heinlein, Burns, and Werker (2010) found that newborn infants 0-3 days old that were exposed to multiple first languages through having bilingual mothers showed no preference for either language postnatally. However, unlike the quail chicks in this series of experiments, the bilingual infants have the benefit of ongoing postnatal exposure to those languages, with the added benefits of auditory-visual redundancy and social contingencies. Without any postnatal auditory enrichment, chicks in this study quickly honed in on their species-typical preference likely through exposure with their conspecific broodmates and their own vocalizations. By 48hr after hatch, chicks across all 4 conditions in Experiment 1 had developed a species-typical preference, indicating

the importance of postnatal exposure with conspecifics. Perhaps with a postnatal reminder or training, quail chicks that received prenatal auditory enrichment would be more malleable to postnatal exposure. Harshaw and Lickliter (2011) found that prenatal exposure of bobwhite quail embryos to a maternal call of a different species made postnatal contingency training of that same call more effective than postnatal training alone. In humans, targeted training in non-native stimuli can increase perceptual discrimination into later infancy and childhood. From foreign human languages (Kuhl et al., 2003) to primate vocalizations (Friendly, Rendall, & Trainor, 2013B), postnatal training can temporarily increase sensitivity to a variety of non-native contrasts. However, this increased sensitivity only lasts as long as the environment continues to provide this increased variation, supporting that perceptual narrowing window.

Experiment 2 was conducted to assess whether the same prenatal auditory enrichment regime would affect response to a novel auditory stimulus, an acoustically distinct call of a fourth quail species. Experiment 1 demonstrated that prenatal auditory enrichment can interfere with the emergence of the species-typical preference, Experiment 2 looked at how the enrichment could generalize to auditory stimuli outside of the original range of exposure. It was predicted that quail chicks that received the Quail Mix prenatally would have no preference for either their species typical call or a novel call. However, chicks in the enriched conditions had an increased openness to novelty and significantly preferred the novel quail call at 24hr following hatching. A variety of enriched rearing paradigms have demonstrated how enrichment impacts emotional reactivity and improves response to novelty (Cymerblit-Sabbag et al., 2013). Previous work with domestic chicken embryos given musical enrichment prenatally

showed increase in a variety of neurological factors associated with auditory function, increased plasticity, and neural survival (Alladi, Roy, Singh, & Wadhwa, 2005B; 2005B; Chaudhury & Wadhwa, 2009; Wadhwa, Anand, & Bhowmick, 1998). Although there are practical limitations to providing auditory enrichment to mammals developing in-utero, studies of rats have found that prenatal auditory enrichment increases their performance on auditory discrimination tasks postnatally, even when those tasks consisted of stimuli outside of the range of the prenatal stimulation (Xu et al., 2009). In a rare study of prenatal auditory enrichment with human mothers and their fetuses, Blum (1998) found that a specific musical auditory-vestibular enrichment program influenced not only postnatal language development but also broader sensiomotor development. However, all of the aforementioned prenatal enrichment studies focused on how music influenced neurobiological and behavioral tasks, which in the case of domestic chickens and rats, is not ecologically valid. The current study used more ecologically valid prenatal auditory enrichment to investigate the phenomenon of perceptual narrowing.

Working with bilingual human infants, Byers-Heinlein, Burns, and Werker, (2010) found that exposing infants to increased variation generalized to a preference for a third, novel language. Bilingual (auditory enriched) infants had an increased openness to new linguistic experiences compared to their monolingual counterparts. In Experiment 2 of the current study, there was a similar effect, in that the prenatal auditory enriched chicks had a significant preference for a novel call at 24 hours following hatch. However, as in Experiment 1, the effects of prenatal auditory enrichment in Experiment 2 on behavioral responsiveness to novelty was also short-lived. By 48hr following hatch, chicks in the prenatal auditory enrichment group had recovered from their prenatal

exposure and preferred the bobwhite maternal call and had become statistically indistinguishable from control chicks that had received no manipulated stimulation.

Social interaction is rich in synchronous multisensory information, and it is this information that builds the foundation for social aptitudes skills as language development and facial recognition (Lewkowicz, 2014). Similarly, the process of perceptual narrowing occurs both for the individual sense modalities as well as for multisensory processing and integration. Because perceptual narrowing occurs most prominently in socially-derived stimulation and because that stimulation is multimodal in nature, it has led some to suggest that perceptual narrowing predominantly occurs for the properties of stimulation that the senses share, such as tempo, rhythm, and intensity (Pascalis et al., 2014).

Experiment 3 assessed the possibility that perceptual narrowing occurs through exposure to the amodal properties of stimulation.

According to the Intersensory Redundancy Hypothesis, multimodal synchronous presentation of a stimulus improves learning and memory through selective attention to the amodal properties of stimulation. Conversely, unimodal presentation of a stimulus recruits attention to the modality specific properties. Therefore, by comparing unimodal and bimodal synchronous presentations of the Quail Mix enrichment regime, we can begin to explore which properties of stimulation early perceptual narrowing depends on more heavily. Results in the current study indicated that chicks that received the Quail Mix with a synchronous pulsed light (Bimodal Synchronous Quail Mix) did not perform significantly different from Control chicks and had a significant preference for the species typical call at 24hr following hatch. Chicks in the Bimodal Synchronous condition showed no evidence of altered perceptual narrowing despite having amassed

approximately 36 hours of synchronous auditory/visual enrichment. This is in contrast to the unimodal auditory and bimodal asynchronous chicks, which did not have a preference for any call at 24hr following hatch. These results indicate that intense multimodal synchronous presentation was not effective and suggests that auditory perceptual narrowing requires access to the modality specific acoustic properties. The results of Experiment 3 can be likened to the results of Radell and Gottlieb (1992), wherein increased amounts of redundant bimodal stimulation interfered with the learning and memory of modality specific properties prenatally. Previous human and comparative research has presented mixed results on whether perceptual narrowing is primarily facilitated by amodal versus modality specific properties. Experiment 3 demonstrated that amodal properties are a key feature of stimulation during prenatal sensory development, in that I found that interfering with the selective attention and learning of those properties made the enriched stimulation to appear ineffective. While this contradicts the current presumption of perceptual narrowing being shaped by amodal information (Pascalis et al., 2014), it is consistent with previous research focused on how precocial birds indentify their species-typical maternal calls in the absence of direct exposure to an adult call (Gottlieb, 1971, 1978, 1984; Gottlieb & Vandenberg, 1968). Many species of precocial birds are able to identify their species-typical maternal call with only exposure to their own vocalizations as an embryo or chick and/or those of same aged peers. These chick vocalizations do not share the same prosody or rhythmic structure as the mother's, but still chicks reliably develop a species-typical preference for the maternal call. In bobwhite quail, exposure to conspecific chick contentment calls prenatally is key to forming postnatal auditory preferences (Sleigh, Columbus, & Lickliter, 1996). Therefore,

there must be modality specific acoustic similarities, such as pitch or timbre, between the chick and maternal calls that guide the development of this preference.

Similarly, in human infants, Tyler, Best, Goldstein, and Antoniou (2014) suggest that the perceptual narrowing of consonants is facilitated by the infant's ability to produce certain sounds using different articulatory organs. Therefore, through self-stimulation the infant becomes particularly adept at noticing differences in those phonemes, and this experience is constrained by their typical articulatory architecture (Tyler et al., 2014). That is not to say that amodal properties of stimulation are never used for perceptual narrowing, it simply suggests that early perceptual narrowing may rely more heavily on these modality specific properties initially. As young organisms develop and become experienced perceivers, different properties of stimulation may become more important over time or as the perceptual discrimination task becomes more difficult (Valliant, 2012). For example, Lewkowicz and Pons (2013) found that human infants are only able to identify their language through amodal properties after perceptual attunement for the modality specific properties of audio and facial stimuli had occurred. That is, before the infants were able to successfully integrate and make accurate discriminations of amodal properties of communication, they had already honed in on the unique, individual properties of each sense modality separately, typically by 10-12 months. When the infants were able to make amodal identification of communication, they did so only in respect to their native language (Lewkowicz & Pons, 2013). Different properties of stimulation may be more important or salient throughout perceptual development, as previous work on phoneme discrimination (Weker & Tees, 2005) shows a sharp decline during this time.

Experiment 3 provided a particular combination of environmental factors that were able to increase the longevity of the effects of prenatal auditory enrichment. The Bimodal Asynchronous group was implemented to provide chicks the same total amount of stimulation as the Bimodal Synchronous group, but without the key feature of temporal synchrony. It was expected that this group would behave similarly to the unimodal Quail Mix chicks, since the audio and light exposure were separate events. However, chicks that received the Quail Mix and the extraneous, asynchronous pulsed light prenatally continued to demonstrate no postnatal preference at 48hr after hatch, an additional day beyond any of the other conditions. This finding suggests that the unusually early light exposure, independent of the auditory enrichment, somehow interfered with postnatal learning, thereby increasing the duration of malleability provided by the Quail Mix soundtrack. In precocial birds, prenatal light exposure has been shown to interfere with the development of the auditory system and impair auditory learning (Gottlieb, Tomlinson, & Radell, 1989). Since the auditory system develops prior to the visual system in birds and mammals, unusually early light exposure can have enduring effects on auditory learning and discrimination.

Limitations

The prenatal auditory and bimodal auditory-visual stimulation provided the embryos in the study was uncharacteristic of their natural rearing circumstances. All calls used in the study were pre-recorded versions of the bobwhite, Japanese, California, and scaled quail maternal calls that have been edited for clarity and duration. The stimulus consisted of repetitions of the same sequence, each approximately 5 seconds long, in blocks of 30 seconds, presented in alternating patterns for a total of 10 minutes of

stimulation. While the maternal assembly call of a hen would have strong similarities between repetitions in the wild (the same “voice” and rhythmic pattern) it would likely never appear in quite the same way each and every time. Yet, despite the lack of variability within each species call, chicks given the Quail Mix prenatally failed to demonstrate a preference for any call they were exposed to at 24 hours after hatch. Chicks in the species-typical (bobwhite) or species atypical (Japanese) prenatal stimulation conditions trended to prefer the exact call that they had heard prenatally. Therefore it would be interesting to provide chicks prenatally with a variety of different calls from their species, not just one exemplar repeated consistently.

Secondly, the bimodal presentations were not ecologically valid. Naturally, the sound of the hen would be paired synchronously with other sense modalities, most notably the vestibular sensations of the mother hen as she calls out. However, Experiment 3 used a visual pairing, a pulsed light, in order to maintain a high degree of experimental control. The pulsed light was chosen due to its ability to make precise, punctuate, and discrete presentations with the audio stimuli, something that would have been difficult if using vibration. Despite the pairing of the pulsed light and the auditory stimulation being uncharacteristic, the effect of the bimodal presentations was evident. In accordance with the Intersensory Redundancy Hypothesis, bimodal synchronous presentation interfered with the learning and memory of the amodal properties of the experimental auditory stimulus (the Quail Mix), resulting in the bimodal synchronous chicks being indistinguishable from controls during testing.

Another issue of ecological validity was present in the postnatal rearing environment of the chicks used in the current study. A bobwhite quail chick’s ontogenetic

niche would consist of approximately a dozen broodmates, a mother hen, and a variety of other species cohabitating the same area. In the current study, chicks were housed in a common laboratory rearing room. While the chicks in the current study were segregated in their own plastic bins, they were exposed to the sounds of approximately 150 other same-age birds housed in the same small room that were being used for other projects. Therefore, the chicks for the current project not only heard themselves and other chicks who received the same prenatal stimulation, they also heard birds from other projects with unique prenatal histories.

The typical ecological niche of a bobwhite quail chick would also include an array of natural physical objects and events, such as grass, rocks, weather, etc. In the current study, chicks were housed in small plastic bins, provided with food, water, and a foam-rubber liner. This combination of an excess species-typical acoustic stimulation and a lack of other kinds of natural enrichment may have provided the birds with an altered perceptual milieu similar to those described for pre-term infants by Rand and Lahav (2014). While the prenatal environment was highly controlled and provided diverse auditory enrichment designed to prevent perceptual narrowing, the postnatal housing of the birds provided both augmented amounts of species-typical experience while being simultaneously eliminating of most other forms of stimulation typically found in the wild.

While it was expected that the chicks would hone in on their species-typical call quickly after hatch with experience from their broodmates, just how quickly the chicks “recovered” from a long history of prenatal auditory enrichment was startling. Perhaps given more ecologically valid postnatal rearing conditions, the perceptual narrowing process may have gone at a different pace.

Future Directions

While perceptual narrowing may be delayed by prenatal auditory enrichment, the duration of that effect appears to be short lived as the young organism accrues experience in its postnatal environment. Future research on perceptual narrowing can look to extend the initial effects of prenatal auditory enrichment, either by providing a similarly diverse postnatal environment, by restricting native exposure, or by interfering with postnatal learning mechanisms. Future studies may also include a longitudinal investigation to see if perceptual narrowing uses different sensory properties as the organism develops and gains more specificity. Although the current study suggests early perceptual narrowing occurs via the modality specific properties of stimulation, do amodal properties (those that are shared between senses) become more important after the young organism has accrued experience and becomes a more sophisticated perceiver?

Perceptual narrowing is by definition a regressive process, but by no means is it a process that can be indefinitely postponed. The young organism must quickly hone in on native distinctions, at the expense of being able to make nuanced distinctions to environmentally rare stimuli, in order to have appropriate social skills and sophistication. By understanding how to slow the course perceptual narrowing, we can also better understand how to facilitate it.

Summary

Perceptual narrowing is a regressive neural pruning and behavioral discrimination process in which young organisms rapidly hone in on the nuanced distinctions between environmentally relevant stimuli at the expense of being able to make nuanced distinctions between non-native stimuli. From a tentatively broad range of sensitivity, the

young organism accrues experience in an ontogenetic niche and specializes to the particular stimuli therein, and if left unaltered, leads the organism towards species-typical preferences and behaviors. Perceptual narrowing has been shown to be a domain-general, pan-sensory process that occurs across senses for a variety of predominantly social phenomenon, including language acquisition, facial recognition, and intersensory processing (Lewkowicz, 2014; Scott, Pascalis, & Nelson, 2007).

The experiments conducted in the current study demonstrate that prenatal auditory enrichment can alter the perceptual narrowing window, the emergence of species-typical auditory preferences, and postnatal response to novelty, at least temporarily. Results also suggest that while perceptual narrowing is considered a domain-general, pan-sensory process, early perceptual narrowing primarily occurs through the modality specific properties available in an individual sense. The current series of experiments contributes to a better understanding of how prenatal and early postnatal environmental affordances and constraints mold the development of species-typical auditory preferences. I found that diverse prenatal auditory enrichment can interfere with the emergence of postnatal auditory preferences and increase openness to novel stimuli of the same class. Inappropriate or unconnected environmental stimulation such as unusually early rhythmic light exposure increased the duration of the altered perceptual window by impairing species-typical learning later into the postnatal environment.

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Sternglanz, R.W., Young, M., Alsip, K., Makiyil, J., & O'Dowd, B. (2014). Can people detect deception from thin slice communications? Poster presented at the 15th annual meeting of the Society for Personality and Social Psychology, Austin, TX, Feb. 2014.

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