

**Effects of Prenatal Sensory-Evoked Arousal on Postnatal Behavior and Perceptual
Responsiveness in Bobwhite Quail (Colinus virginianus)**

by

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(ABSTRACT)

Prenatal sensory stimulation can have facilitative or interfering effects upon subsequent perceptual learning and development in bobwhite quail. Exposure to moderate amounts of prenatal unimodal sensory stimulation has been shown to accelerate early intersensory responsiveness, while exposure to concurrent prenatal bimodal sensory stimulation has been shown to interfere with perceptual learning and development. An immediate mechanism that may underlie this developmental intersensory interference is the arousal level of the organism associated with exposure to prenatal bimodal stimulation. Concurrent prenatal bimodal stimulation is known to elicit significantly higher levels of behavioral arousal and heart rate in bobwhite quail embryos. This study investigated the possibility that increased arousal associated with prenatal bimodal stimulation could have enduring effects upon subsequent postnatal behavioral organization and perceptual abilities in bobwhite quail.

Subjects were exposed to one of three prenatal stimulation regimes: (a) concurrent bimodal (auditory/visual) stimulation, (b) unimodal auditory stimulation, or (c) no supplemental stimulation. Chicks exposed to concurrent prenatal bimodal stimulation demonstrated significantly greater levels of behavioral activity as well as decreased social behavior in the open-field when compared to unimodal auditory subjects and controls. Additionally, prenatal bimodal exposure may have led to a failure to utilize multimodal maternal cues in determining species-specific perceptual preferences in the days following hatching. All exposure groups demonstrated postnatal auditory learning of a maternal call, thus no interference effect was found for concurrent prenatal bimodal stimulation on postnatal auditory learning. These results suggest that concurrent prenatal bimodal stimulation has enduring effects upon postnatal behavioral arousal that may impact perceptual responsiveness of bobwhite quail in the days following hatching.

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Introduction

Over the course of the past century, a great amount of time and effort has been invested in theory and research on the construct of attention. Two of the more common approaches that have emerged in the study of attention have focused on “attention as selectivity” and “attention as state” (Ruff & Rothbart, 1996). “Attention as selectivity” refers to an organism’s selection of external or internal events as the object of attention. “Attention as state” refers to the physical state of an organism that is associated with attention as selectivity (or the act of attending). These two attentional constructs are tightly intertwined, having strong bidirectional influences on one another. Not only does the process of selective attention influence the state of the organism, in addition, the state of the organism influences an organism’s attentional selectivity (Gardner & Karmel, 1995; Richards & Casey, 1991).

Attention and Arousal

A large body of research with human subjects has been aimed at uncovering possible links between arousal and attention. Sokolov (1963) suggested that attention is initiated through an orienting response. The orienting response is composed of specific behavioral reactions, as well as changes in central and autonomic nervous system activity that reflect alterations in the organism’s general level of arousal. These alterations in arousal level are associated with attending to an environmental stimulus. Sokolov (1963) argued that these physiological responses amplify or reduce the effects of sensory stimulation by acting directly on sensory receptors and indirectly through feedback to central mechanisms, ultimately having major effects on learning and perceptual processes. Lacey and Lacey (1958) found that increased heart rate was associated with inhibition of cortical activity. The authors proposed that this physiological response was likely to occur in situations where stimulation is unpleasant or painful, thus facilitating a “rejection” of environmental information. However, in situations where attention is called for, decreases in heart rate associated with increased sensitivity to stimulation are found to occur (Lacey, 1959; Lacey, Kagan, Lacey, & Moss, 1962). In other words, decreased heart rate is associated with a decrease in sensory thresholds, and increased heart rate is associated with an increase in sensory thresholds. Subsequent research has

led to a more sophisticated understanding of the relationship between heart rate and attention.

Richards and Casey (1991, 1992) found that heart rate appears to coincide with various phases of visual attention in human infants. During stimulus orienting, which is synonymous with Sokolov's (1963) orienting response, infants exhibit a large deceleration in heart rate that is believed to be associated with the early stages of information processing. Following stimulus orienting, there is a period of sustained attention. This phase of attention is represented by a sustained decrease in heart rate and heart rate variability, and decreased motor activity. Sustained attention is associated with active processing of environmental information. The last phase of attention is attention termination, in which the infant may continue to display behavioral signs of attention (i.e., visual fixation); however, heart rate returns to baseline levels. Infants are least distractible during sustained attention, taking the longest time to look toward a distractor stimulus during this period of decreased heart rate (Casey & Richards, 1988). In addition, infants' memory for a stimulus is improved when presentation occurs during sustained attention as opposed to attention termination (Richards, 1997). These findings provide strong support for increased attention and processing of environmental information during periods of decreased heart rate.

Richards and Hunter (1998) proposed that the relationship between heart rate and visual attention systems may reflect a common underlying system of reciprocal connections involving a "cardioinhibitory system" in the frontal cortex, the limbic system, and the mesencephalic reticular activating system (Heilman, Watson, Valenstein, & Goldberg, 1987; Mesulam, 1983). Stimulation of the reticular activating system evokes low voltage high frequency desynchronized electrical activity throughout the cortex that is associated with alert wakefulness and vigilance (Moruzzi & Magoun, 1949; Starzl, Taylor, & Magoun, 1951). Other components of this system are involved in auditory and visual perception, and attention (Posner, 1995; Posner & Petersen, 1990). Thus, a certain pattern of physiological and behavioral reactions across multiple levels of the developmental system occurs during sustained attention that is associated with increased processing of environmental information (Berg & Richards, 1997).

Vagal tone is of particular interest to many scientists in this area of study. Vagal tone refers to heart rate variability that is controlled by the parasympathetic nervous system. Specifically, the 10th cranial (or vagus) nerve innervates the heart and various organs of the thoracic and abdominal cavities supplying these organs with parasympathetic information. The dorsal motor nucleus of the vagus nerve is responsible for decelerations of heart rate, and the nucleus ambiguus of the vagus nerve is responsible for maintaining heart rate variability (Reed, Ohel, David, & Porges, 1999).

Low vagal tone refers to low baseline variability in heart rate. Greater baseline heart rate variability (i.e., high vagal tone) is considered an indication of fetal well-being (Kruse, 1982), and is associated with an organism's ability to attend and subsequently respond to features of the external environment (Richards & Casey, 1991). Heart rate variability and overall heart rate decline when an organism attends to environmental stimuli (Porges & Raskin, 1969), a lack of decrement in heart rate indicates low attention. Individuals with low vagal tone consistently perform worse than those with high vagal tone on habituation tasks, discrimination tasks, and cognitive assessments (Fox & Porges, 1983; Porges, 1992).

Richards (1987) has argued that the variability in heart rate that coincides with respiration, termed respiratory sinus arrhythmia (RSA), is the best indicator of the influence of vagal tone on attention. RSA is under the control of the respiratory centers of the brain stem (i.e., pons and medulla), and the vagus nerve is also influenced by activity in the frontal lobes. Dykman and colleagues (1971) proposed that an inhibitory system in the forebrain exerts control over the reticular activating system. Deficient inhibition of the reticular activating system leads to intolerable "signal-to-noise" ratios at the cortical levels. This deficient activity of the cardioinhibitory system in the frontal cortex may be associated with the development of attention deficit hyperactivity disorder. The ability to attend is key to learning about and responding to an organism's surrounding environment, and is therefore key to the organism's adaptation and survival. Thus, the link between arousal and attention may play a pivotal role in an organism's early perceptual and behavioral development.

Gardner and Karmel (1995) found that the relationship between arousal and attention is bidirectional. In a longitudinal study, looking preferences were examined when infants were: newborns, 1 month, and 4 months of age. Infants' preference for low, medium, or high frequency visual stimulation was assessed while less aroused (after feeding), more aroused-internal (before feeding), and more aroused-external (after feeding but with exposure to augmented visual stimulation before each trial). The results revealed that during the newborn period and at 1 month of age, infants preferred faster visual stimulation when less aroused and slower visual stimulation when more aroused. Interestingly, the preference for slower stimuli when more aroused held regardless of arousal condition (external or internal). By 4 months of age, infants preferred faster stimuli under all arousal conditions, indicating that the link between arousal and attention may be strongest in early development. The tight link between arousal and attention in early development may play a key role in the developing organism's perceptual organization and early perceptual learning.

Intersensory Perceptual Development

A consistent finding from studies of prenatal and perinatal perceptual development relates to the sequential onset of functioning in sensory systems. All avian and mammalian species studied to date follow the same invariant and sequential pattern of functional onset (tactile – vestibular – chemical – auditory – visual; Alberts, 1984; Gottlieb, 1971a). Although the specific time of functional onset of each sensory system varies from species to species, studies suggest an overall pattern of relationship between sensory systems during prenatal and early postnatal development that appear to apply across species. Prior to birth or hatching, all avian and mammalian embryos have experienced limitations on sensory input due to the sequential onset of the various sensory systems during prenatal development. We now know that each sensory system develops within its own unique time frame, and that the stimulative history of individual sensory systems can affect the development of the other sensory systems, thereby shaping the organism's early perceptual organization (see Lickliter & Banker, 1994).

A number of studies utilizing animal embryos and infants have demonstrated that the type, amount, and timing of prenatal sensory stimulation affects perceptual learning

and perceptual preferences (reviewed in Lickliter, 2000). Whether prenatal sensory experience leads to facilitation or interference of early perceptual development appears to depend upon a number of factors related to quantitative and qualitative aspects of the stimulation provided, as well as the state of the organism at the time of stimulation. For example, Lickliter (1990) found that providing bobwhite quail embryos with moderate levels of visual stimulation had a facilitating effect on the bobwhite chicks' intersensory perceptual development. Quail embryos exposed to 10 min/hr of patterned visual stimulation during the final 24 hour period leading up to hatching utilized a combination of auditory and visual cues when determining their perceptual preferences at an earlier age than normal control chicks. Normally reared bobwhite chicks show an initial reliance upon auditory cues (a bobwhite maternal call) when directing their perceptual preferences for the first 48 hours following hatching, but by 72 hours of age, normally-reared chicks require a combination of auditory and visual information (a bobwhite maternal call paired with a stuffed bobwhite hen model). In contrast to this normal trend in developmental timing, chicks exposed to prenatal visual stimulation required the combination of auditory and visual cues at both 24 and 48 hours following hatching to display a preference for species-specific perceptual cues. A subsequent study demonstrated that exposure to moderately enhanced levels of prenatal auditory stimulation had a similar facilitative effect for bobwhite quail chicks (Lickliter & Stoumbos, 1991).

However, substantially augmented prenatal sensory stimulation appears to interfere with the development of species-typical perceptual preferences. Sleigh and Lickliter (1995) exposed bobwhite quail embryos to 40 min/hr of patterned visual stimulation during the 24 hour period prior to hatching. In stark contrast to the facilitative findings of 10 min/hr of visual stimulation found in Lickliter (1990), these chicks failed to utilize combined auditory-visual cues in directing their perceptual preferences at all ages tested (i.e., 24, 48, 72, and 96 hours post-hatching). This finding clearly demonstrates that substantially *increasing* the amount of prenatal sensory stimulation available to the developing organism can interfere with species-typical perceptual development (see also Carlsen & Lickliter, 1999).

On a similar note, it appears that substantially *decreasing* the amount of stimulation available to the developing embryo also leads to an interference of early perceptual development. Gottlieb (1993) investigated the effects of attenuated prenatal tactile stimulation on prenatal auditory learning in mallard duckling embryos. Ducklings deprived of the tactile stimulation normally provided by broodmates (by means of physically isolated incubation) were unable to demonstrate learning of a maternal call they had been exposed to as embryos. Ducklings incubated in normal conditions allowing tactile and vestibular stimulation were able to demonstrate prenatal learning of a maternal call. Lickliter and Lewkowicz (1995) found that isolated incubation also interfered with prenatal learning of a maternal call for bobwhite quail embryos. Interestingly, embryos incubated in isolation that were exposed to 10 min/hr of visual stimulation were able to demonstrate learning of a maternal call they were exposed to prenatally. The authors concluded that the overall arousal level associated with prenatal sensory experience may play a role in its subsequent effects upon prenatal perceptual learning and postnatal filial behavior. Attenuated tactile stimulation may have led to levels of arousal that fell below some optimal range, while the augmented visual stimulation served to increase arousal to a level more typically found in the prenatal ecology of the bobwhite. From this perspective, the species-typical prenatal environment is seen to provide the developing organism with an optimal level of sensory stimulation, thereby fostering an optimal level of arousal for early perceptual development (Radell & Gottlieb, 1992).

Turkewitz and Kenny (1982, 1985) suggested that the sequence of functional onset in sensory systems serves to reduce competition between emerging sensory modalities. The typical milieu of a developing embryo or fetus is buffered from simultaneous sensory stimulation from multiple sensory modalities. This buffered environment may be critical to species-typical perceptual development, in that it shelters the organism from exposure to overwhelming amounts or combinations of sensory exposure. For example, according to Turkewitz and Kenny's (1982, 1985) hypothesis, premature sensory stimulation of a late developing sensory system (visual) interferes with normal development of an earlier developing system (auditory) by providing too much

competition for the young organism's underdeveloped attentional capacities. Limitations of sensory input serve to reduce the attentional demands placed on the embryo or fetus.

Several studies have provided support for Turkewitz and Kenny's developmental intersensory interference hypothesis. Providing embryos with concurrent multimodal stimulation has been found to have detrimental effects on prenatal perceptual learning and postnatal filial behavior. Gottlieb, Tomlinson, and Radell (1989) exposed mallard duck embryos to an individual mallard maternal call concurrently with exposure to visual stimulation. Embryos exposed to this concurrent stimulation regime showed no preference for the familiar maternal call versus an unfamiliar maternal call in postnatal testing. In contrast, another group that had been exposed to non-concurrent (alternating) presentations of an individual maternal call and patterned light did display a preference for the familiar call during postnatal testing. Studies utilizing bobwhite quail have yielded similar results, supporting the proposal that concurrent bimodal stimulation somehow serves to disrupt normal perceptual learning (Honeycutt & Lickliter, 2001a; Lickliter & Hellewell, 1992). Radell and Gottlieb (1992) also showed that concurrent stimulation of an earlier developing system (vestibular) along with a later developing sensory system (auditory) resulted in this interference effect. Thus, the specific sensory modalities involved in concurrent bimodal stimulation may not be as important as the overall effect of simultaneous exposure to two sources of sensory information. Once again, the combination of multiple sources of information provided by bimodal stimulation may lead to an increase in arousal levels that exceeds an optimal range for species-typical perceptual learning and development.

Comparative Studies of the Role of Arousal in Early Development

If arousal is so tightly intertwined with attention and perception in early development, it is possible that early perceptual experience may have the capacity to impact arousal in a sufficient manner to alter the organism's overall perceptual development and behavioral organization. Schneider, Kraemer, and Suomi (1991) exposed rhesus monkey infants to moderate amounts of vestibular-proprioceptive stimulation in the first month of postnatal life. At eight months of age, these monkeys performed better than controls on motor and problem solving tasks. Furthermore,

subjects exposed to augmented sensory stimulation as neonates demonstrated more favorable responses to novel situations than control subjects. This moderate amount of stimulation may have fostered levels of arousal optimal for early perceptual and motor development.

Although there is little direct evidence linking prenatal sensory-evoked arousal and postnatal behavioral development, there is evidence that prenatal stress affects postnatal behavior. The stress reaction is composed of multiple components involving: the behavioral system, the hypothalamo-pituitary-adrenocortical axis, the sympatho-adrenomedullar axis, the immune system, the endogenous opioid system, and the cardiovascular system (Schrader & Ladewig, 1999). Schneider (1992) investigated the effects of mild prenatal stress on neuromotor maturation in rhesus monkeys. To induce prenatal stress, pregnant rhesus monkeys were isolated and exposed to unpredictable noise stimuli. Infants exposed to prenatal stress exhibited lower scores on a motor maturity index and higher distractibility ratings than non-exposed infants. Similarly, rats exposed to a stressor as fetuses (e.g., maternal restraint) have been shown to demonstrate higher rates of ultrasonic vocalizations during isolation or confrontation with a novel environment, as well as greater movement than controls when tested in the open-field (Williams, Hennessy, & Davis, 1998; Vallee, Mayo, Dellu, LeMoal, Simon, & Maccari, 1997). The authors' suggested that early alterations of the hypothalamo-pituitary-adrenal (HPA) axis induced by environmental experience had influenced postnatal adaptability and behavioral reactivity of the rats exposed to prenatal stress. These studies indicate that changes in fetal state may have effects that continue to impact the organism's development in postnatal life.

Investigators have drawn from the wealth of findings in the human research literature on arousal and attention in designing comparative studies of early perceptual development and learning. These studies have utilized aspects of the orienting response (e.g., behavioral activity and measures of heart rate) as an index of attention and perceptual sensitivity in a variety of species at various times in development. Findings similar to those in the human literature have emerged from these comparative studies of the orienting response.

Hayne, Richardson, and Campbell (1991) investigated the development of behavioral and heart rate orienting responses to olfactory stimulation in neonatal rat pups. Behavioral activity and heart rate was measured before and during exposure to an olfactory stimulus in rat pups that were 1, 3, 6, 9, and 12 days of age. Behavioral orienting (sniffing and general increases in behavioral activity) was observed in rats at all ages tested; however, reliable decreases in heart rate were not observed until day 9. However, in a subsequent experiment, subjects were anesthetized with haloperidol to reduce stimulus-elicited motor activity. Under these conditions, decreased heart rate during exposure to the olfactory stimulus was observed at earlier ages, leading the authors to conclude that behavioral activity had masked the heart rate orienting response of the rats at younger ages. The link between motor activity and heart rate is termed cardiosomatic coupling, and based upon these findings, it appears to change with age in rats.

Ronca and Alberts (1990) measured heart rate in rat fetuses and pups during exposure to gustatory stimulation. Lemon extract was delivered to the subjects through an intraoral cheek cannula with heart rate being measured for 1 minute prior to stimulus exposure and 1 minute following stimulus onset. Subjects in all age groups showed significantly decreased heart rate during stimulus exposure. In addition, rat pups showed increased behavioral activity during exposure periods; however, no measure of behavioral activity was utilized during prenatal exposure sessions. Smotherman and Robinson (1988) found that rat fetuses show increased behavioral activity during chemical stimulation as early as day 19 of gestation. These studies demonstrate that rat pups and fetuses do display orienting responses to chemical stimulation. Similarly, fetal sheep display differential responding to intraoral catheter injections of milk or quinine (Robinson, Wong, Robertson, Nathanielsz, & Smotherman, 1995). Exposure to quinine is associated with increases in heart rate, while exposure to milk is found to elicit decreases in heart rate.

Taken together, these findings are not surprising given that the chemical senses develop relatively early, and given that these studies utilized unimodal sensory stimulation for stimulus exposure. Several studies have shown that young organisms can

process information provided unimodally but fail to process information provided by concurrent bimodal stimulation (Gottlieb, Tomlinson, & Radell, 1989; Honeycutt & Lickliter, 2001a; Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992). Bimodal stimulation may lead to an increase in arousal levels that exceeds an optimal range for perceptual learning.

Reynolds and Lickliter (in press) tested this hypothesis in an investigation of the effects of prenatal sensory stimulation on behavioral and physiological arousal in bobwhite quail embryos. Embryos were videotaped during initial exposure to: concurrent bimodal stimulation (concurrent exposure to patterned light and an individual maternal call), concurrent intramodal stimulation (two different maternal calls), unimodal auditory stimulation (an individual maternal call), unimodal visual stimulation (patterned light), or no supplemental stimulation. An additional experiment utilized the same stimulus exposure groups and measured heart rate prior to, during, and following stimulus exposure. Bimodal stimulation was found to elicit significantly higher levels of behavioral and physiological arousal in subjects when compared with other exposure conditions. Embryos exposed to bimodal stimulation showed significantly greater increases in behavioral arousal (activity level) during stimulus exposure, as well as significantly greater changes from baseline heart rate during exposure periods than all other exposure groups and controls. Subjects exposed to unimodal auditory stimulation did not exhibit a significant change in heart rate during stimulus exposure. This is consistent with the previously demonstrated ability of bobwhite quail embryos to demonstrate prenatal auditory learning under unimodal exposure conditions (Honeycutt & Lickliter, 2001a; Lickliter & Hellewell, 1992).

A subsequent study explored the effects of prolonged exposure to prenatal sensory stimulation on heart rate in bobwhite quail embryos (Reynolds, Honeycutt, & Lickliter, 2002). Embryos were exposed to 10 min/hr of concurrent non-synchronized audio/visual stimulation, concurrent synchronized audio/visual stimulation, unimodal auditory stimulation, or no supplemental stimulation for six hours (a total of 60 min) during the 24 hour period prior to hatching. Following the exposure period, embryos heart rate was measured before, during, and following a final exposure session. Embryos

in the concurrent non-synchronized multimodal group had significantly higher baseline heart rate than subjects in all other groups and displayed significantly greater changes from baseline during stimulus exposure. Interestingly, embryos exposed to synchronized bimodal stimulation resembled controls and unimodal exposure subjects on both baseline and change from baseline measures of heart rate. This finding suggests that synchronized bimodal stimulation may be perceived as a single event (see Spear & McKinzie, 1994). Taken together, these studies provide support for the notion of some optimal level of arousal associated with species-typical prenatal experience that fosters species-typical perceptual development. Not only did one-time exposure to concurrent bimodal stimulation elicit high levels of behavioral and physiological arousal in bobwhite embryos, 6 hours of moderate amounts of bimodal stimulation resulted in embryos displaying significantly elevated baseline heart rate during the absence of stimulus exposure and significant tachycardia during their seventh exposure to the bimodal stimulation.

The findings of Reynolds, Honeycutt, and Lickliter (2002) indicate that embryos exposed to prenatal bimodal sensory stimulation have significantly higher baseline heart rate following seven hours of intermittent stimulus exposure. This illustrates an enduring effect of sensory experience on the physiological state of the organism. It is likely that there are some non-obvious effects that may stem from a sustained period of high arousal elicited by prenatal bimodal stimulation. High levels of arousal are known to be associated with increased behavioral activity and vocalizations in precocial avian species (Gottlieb, 1971 b; Gray, 1990). Therefore, it is plausible that chronically aroused bobwhite chicks would display consistently higher levels of behavioral activity and vocalizations across a variety of settings than normal bobwhite quail chicks. Sleight and Lickliter (1997) reported that bobwhite quail chicks exposed to substantially augmented levels of prenatal auditory stimulation exhibited high levels of behavioral arousal (as indicated by increased vocalizations), failed to demonstrate species-typical perceptual preferences, and most importantly, had higher mortality rates than chicks that were not exposed to substantially augmented prenatal sensory stimulation. Prenatal perceptual experience that falls beyond some optimal range appears to change the state of the

organism in a manner that has enduring effects not explicitly linked to early perceptual experience.

Statement of Purpose

Prenatal sensory stimulation can have facilitative or interfering effects upon subsequent perceptual learning and development, depending upon the features of the stimulation as well as the developmental history of the organism (Lickliter, 1993, 2000). Exposure to concurrent prenatal bimodal sensory stimulation has been shown to interfere with perceptual learning and development. An immediate mechanism that may underlie this developmental intersensory interference is the arousal level of the organism associated with prenatal bimodal stimulation. The increased arousal associated with prenatal bimodal stimulation could have enduring effects upon the young organism's subsequent behavioral organization and perceptual abilities. Given that several studies have shown that prenatal bimodal sensory stimulation interferes with prenatal auditory learning (Honeycutt & Lickliter, 2001 a; Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992), it seems plausible that there are also other effects on the postnatal behavior of chicks. In other words, alterations in prenatal arousal levels may lead to subsequent modifications in postnatal perceptual and behavioral responsiveness.

The purpose of this study was to investigate the link between the physiological effects of prenatal sensory stimulation (unimodal vs. bimodal) and the postnatal behavior of bobwhite chicks. It was predicted that the high levels of arousal associated with prenatal bimodal sensory stimulation would lead to differences in responding on several postnatal behavioral measures when compared to the responses of chicks exposed to unimodal sensory stimulation or no supplemental stimulation during the prenatal period. In particular, chicks exposed to concurrent bimodal sensory stimulation as embryos were predicted to: (1) demonstrate higher behavioral activity levels, (2) fail to demonstrate postnatal auditory learning, and (3) fail to demonstrate species-typical utilization of multimodal maternal cues in determining social preferences in the days following hatching.

General Method

Subjects

Two hundred sixteen incubator-reared bobwhite quail (*Colinus virginianus*) served as subjects. Fertile, unincubated eggs were obtained weekly from a commercial supplier and set in a Petersime Model I incubator. The incubator was maintained at 37.5 degrees Celsius and 80% humidity. After 20 days of incubation, the eggs were transferred to a hatching tray in the bottom of the incubator. To control for the possible effects of developmental age, only birds that hatched on the 23rd day of incubation were used. Subjects for each group were drawn from at least three batches of eggs to control for between-batch variation. The only sounds embryos were exposed to during incubation were their own vocalizations and those of their siblings, as well as the low frequency background noise emitted from the incubator fan and motor. After hatching, chicks were reared in groups of 10 – 12 to approximate natural brood conditions. The subjects were reared in a sound-attenuated room, illuminated by a 110-W brooder lamp. Ambient air temperature was maintained at 30 degrees Celsius, and food and water was available throughout the duration of the experiments.

Procedure

The bobwhite quail embryo's bill normally penetrates the air space at the large end of the egg on the 21st day of incubation (approximately 24-36 hr prior to hatching). The penetration of the shell produces a visible indentation (or "pip") on the outer shell of the egg. At this time the embryo begins to respire and vocalize (Freeman & Vince, 1974). The embryo's age is calculated on the basis of the first day of incubation being Day 0, the second day of incubation being Day 1, until the embryo hatches. Eggs showing a single pip during the first half of Day 21 were placed in a portable Hovi-bator incubator located in a darkened room. The incubator was manufactured with a Plexiglas top, allowing for observation of the embryos within. In addition, the Plexiglas top was equipped with air-hole openings allowing for the administration of audio and visual stimulation. It has been demonstrated that following movement into the air space in the days prior to hatching, quail embryos respond to auditory and visual stimulation

presented through the egg shell (Carlsen & Lickliter, 1999; Lickliter, Bahrlick, & Honeycutt, 2001).

Prenatal Sensory Stimulation

The auditory stimulus used for prenatal stimulation was a recording of a bobwhite hen incidental call (hereafter referred to as call C). This call was recorded in the field and has been described by Heaton, Miller, and Goodwin (1978). The recording of the call was broadcast to embryos through a Sony compact disk player via an Optimus amplifier connected to a portable speaker located on top of the portable incubator. The sound level of the hen's call was maintained at a maximum peak intensity of 65 dB (A scale, fast response) inside the incubator. This was measured with a Bruel & Kjaer 2232 sound level meter. The visual stimulus used during prenatal stimulation was temporally patterned light produced by a 15-W strobe light pulsing at 1 cycle per second. The strobe light (Realistic Model 42-3009-A) was located immediately above the Plexiglas top of the portable incubator (approximately 4 cm). The bimodal stimulation consisted of the combined and concurrent presentation of the auditory and visual stimuli described above. Amodal properties of the auditory and visual stimuli (e.g., rhythm, rate, intensity) were not temporally synchronized. Embryos were exposed to either: (a) concurrent auditory/visual stimulation, (b) unimodal auditory stimulation, or (c) no supplemental stimulation. The embryos were exposed to 10 min/hr of stimulation for six hours during the last 24 hours prior to hatching. Temperature and humidity were continuously monitored to insure that the presence of the light did not affect the ambient air temperature or humidity of the incubator.

Manipulation Check

Following exposure to prenatal sensory stimulation, heart rate was measured in a sample of subjects (8) from each of the three groups as an index of their physiological arousal. In particular, this measure attempted to replicate the findings of Reynolds, Honeycutt, and Lickliter (2002) which found that embryos exposed to 10 min/hour of concurrent bimodal prenatal stimulation for six hours displayed significantly higher baseline heart rate than embryos exposed to unimodal auditory prenatal stimulation. In order to gain access to the embryos for heart rate recording, a portion of the shell and

inner shell membrane over the air space of the egg was removed. The process of removing the egg and inner egg shell membrane does not affect incubation, survivability, or species-typical perceptual responsiveness (Banker & Lickliter, 1993; Lickliter, 1990). The process takes 1-2 minutes and produces little, if any, bleeding. Subjects were individually placed in a portable incubator for heart rate measurement. Heart rate was recorded using two Biopac 18 gauge unipolar needle electrodes inserted subcutaneously. One electrode was implanted ventrally just below the embryo's right wing, the other electrode was implanted dorsally at the nape of the neck. This procedure is similar to that utilized in previous experiments with rat fetuses (Richardson, Hayne, & Campbell, 1992; Ronca & Alberts, 1990), with slight modifications to accommodate the embryo's position in the shell. The R-spikes were amplified using a Biopac MP100 amplifier and converted to beats per minute (bpm) through the use of AcqKnowledge software. Approximately 30 minutes following the final period of stimulus exposure, heart rate was measured for a one minute period in order to obtain a baseline measure after the embryo had received augmented prenatal sensory stimulation. Baseline heart rate was defined as the average of the subject's mean bpm during the first and last ten seconds of recording.

The results of the manipulation check were significant, $F(2,21) = 3.883$; $p < .05$. The concurrent bimodal exposure group ($M = 281.4013$; $SD = 22.0151$) demonstrated significantly higher baseline heart rate than controls ($M = 261.4202$; $SD = 6.4227$) following stimulus exposure ($p < .05$). The unimodal auditory group ($M = 263.3778$; $SD = 14.9649$) differed significantly on baseline heart rate from the bimodal group at $p < .10$.

Experiment 1: Effects of Prenatal Sensory Stimulation on Postnatal Open-Field Behavior

Past studies from our lab have shown that prenatal sensory stimulation can have immediate, as well as enduring effects on behavioral arousal and heart rate in bobwhite quail embryos (Reynolds & Lickliter, in press; Reynolds, Honeycutt, & Lickliter, 2002; Sleigh & Lickliter, 1997). For example, quail embryos exhibit significantly elevated behavioral activity and heart rate during exposure to concurrent bimodal stimulation. In addition, embryos exposed to concurrent bimodal stimulation for 10 min/hr for six hours exhibit a significantly higher baseline heart rate when compared with embryos exposed to

unimodal stimulation or no supplemental stimulation. These findings suggest that exposure to concurrent bimodal stimulation can lead to a sustained increase in physiological arousal in bobwhite quail embryos.

Whether increased arousal associated with prenatal exposure to concurrent bimodal stimulation continues after hatching remains to be seen. It is plausible that a sustained increase in behavioral and physiological arousal evoked by prenatal sensory stimulation may have more enduring effects upon the young organism's behavioral organization. The purpose of this experiment was to assess behavioral arousal (as measured by open-field behavior) in bobwhite quail chicks that were exposed to modified prenatal sensory stimulation. Subjects were exposed to concurrent bimodal stimulation ($n = 24$), unimodal auditory stimulation ($n = 24$), or no supplemental stimulation ($n = 24$) prior to hatching. Their activity in the open-field was assessed following hatching. It was predicted that subjects in the concurrent bimodal exposure group would display significantly higher levels of behavioral activity than subjects in the unimodal exposure group and control group.

Method

At 24 hours following hatching, subjects were tested in a plastic rearing tub (45 cm long x 25 cm wide x 15 cm high). Subjects were tested in groups of four. A grid pattern of black string was overlaid on the top of the testing tub. This pattern divided the tub into 6 equal rectangular areas measuring 15 X 25 cm. The testing trial lasted 2 minutes and was videotaped with the use of a Panasonic WV-3230 color video camera positioned directly above the testing tub, allowing for later scoring of open-field behavior.

Data analysis

The video taped trials were scored by two independent raters. Two behavioral measures were scored, (a) grid crossing, defined as total number of times an individual subject crossed under the string separating each grid, and (b) huddle duration, defined as total time spent by all 4 subjects within the same grid space. Grid crossing was utilized as a measure of behavioral activity level while huddle duration was utilized as a measure of social behavior. These measures were related; however, the relationship was not an

inverse relationship. It was possible for subjects to freeze in a grid other than the grid/s the other 3 subjects were in. A Fischer Scientific digital counter was used to help ensure accuracy of scoring. The counter provided a reliable means of entering and summing numbers of grid crossings without the interference potentially provided by paper and pencil scoring. As a means of differentiating between each subject during the scoring procedure, differing colored stickers were placed upon the subjects' heads. Pearson product correlations of $\rho = .941$ for the grid crossing measure, and $\rho = .915$ for the huddle duration measure indicated interrater reliability. Group differences in grid crossings and huddle duration were analyzed with one-way ANOVA's. Sub-group comparisons were made with the Tukey HSD post-hoc test as has been suggested for studies with equal cell sizes (Jaccard, Becker, & Wood, 1984). Alpha-level was set at $p < .05$.

Results and Discussion

The results from the analysis of frequency of grid crossings and huddle duration per group are shown in Table 1. The one-way ANOVA on grid crossings was significant, $F(2,69) = 13.78$; $p < .001$. A Tukey HSD post-hoc comparison indicated that the concurrent bimodal group exhibited significantly greater numbers of grid crossings than the control group ($p < .001$) and the unimodal auditory group ($p < .05$, see Figure 1). Figure 2 illustrates the results from the measure of huddle duration. Again, the one-way ANOVA indicated significant differences between groups, $F(2,15) = 3.970$; $p < .05$. The concurrent bimodal group spent significantly less time huddling when compared to the control group ($p < .05$).

These results are consistent with the findings from Reynolds and Lickliter (in press) indicating increased behavioral activity *during* exposure to concurrent prenatal bimodal stimulation. However, these findings are the first to indicate that concurrent bimodal stimulation during the prenatal period can have *enduring* effects upon the postnatal behavioral organization of bobwhite quail chicks. Chicks exposed to concurrent bimodal stimulation as embryos displayed significantly greater activity levels in the open-field in the period following hatching than those exposed to unimodal auditory or no supplemental stimulation as embryos.

In addition to affecting overall behavioral activity level, concurrent prenatal bimodal stimulation appeared to affect social behavior in hatchlings. Chicks exposed to concurrent bimodal stimulation during the prenatal period spent significantly less time huddling with broodmates during testing than unmanipulated control chicks. The increased activity levels associated with concurrent prenatal bimodal stimulation likely contributed to the quail chicks' decreased ability to engage in huddling behavior.

Previous studies have demonstrated that concurrent prenatal bimodal stimulation interferes with the ability of bobwhite quail to demonstrate evidence of prenatal auditory learning (Honeycutt & Lickliter, 2001 a; Lickliter & Hellewell, 1992; for a similar example with ducklings, see Gottlieb, Tomlinson & Radell, 1989). Additionally, concurrent bimodal stimulation has been shown to elicit increased behavioral arousal and significant increases in heart rate in bobwhite quail embryos (Reynolds & Lickliter, in press). This increased arousal during the time of stimulus presentation could serve as an immediate mechanism behind the intersensory interference effect on prenatal auditory learning associated with concurrent bimodal stimulation (Lickliter & Lewkowicz, 1995; Radell & Gottlieb, 1992). The next experiment investigated the possibility that concurrent prenatal bimodal stimulation may also lead to an interference with postnatal auditory learning in quail chicks.

Experiment 2: Effects of Prenatal Sensory Stimulation on Postnatal Auditory Learning

Previous research has demonstrated that bobwhite quail embryos can learn an individual bobwhite maternal call under conditions of unimodal presentation, but fail to demonstrate prenatal learning of a maternal call when it is presented concurrently with patterned visual stimulation (Honeycutt & Lickliter, 2001 a; Lickliter & Hellewell, 1992). Concurrent prenatal bimodal stimulation is known to evoke increased behavioral and physiological arousal in bobwhite quail embryos (Reynolds & Lickliter, in press; Reynolds, Honeycutt, & Lickliter, 2002). The increased arousal level associated with concurrent bimodal stimulation may exceed an optimal level for perceptual learning, possibly disrupting the ability of embryos to selectively attend to features of the maternal call (Radell & Gottlieb, 1992).

If repeated exposure to concurrent bimodal stimulation in the prenatal period leads to elevated behavioral arousal in the immediate postnatal period (see Experiment 1), then auditory learning of a maternal call may also be disrupted in the period following hatching. The purpose of this experiment was to assess the effects of changes in arousal due to prenatal sensory stimulation on postnatal auditory learning in bobwhite quail chicks. It was predicted that subjects exposed to concurrent prenatal bimodal stimulation ($n = 24$) would not demonstrate learning of an individual bobwhite maternal call in the period following hatching. In contrast, it was predicted that subjects from the unimodal exposure group ($n = 24$) and controls ($n = 24$) would demonstrate postnatal auditory learning of an individual maternal call.

Method

Following hatching, chicks were placed in plastic rearing tubs identical in size to the rearing tubs used in Experiment 1. Chicks were housed in groups of 10 – 14 per tub to mimic naturally occurring brood conditions. Subjects were exposed to 10 min/hr of a recorded bobwhite maternal call (call A) for the first 24 hours following hatching.

Method of presentation and maximum peak intensity of the sound level were identical to that used for presentation of prenatal sensory stimulation (see General Method section).

At 48 hours following hatching, chicks were placed individually in a testing arena and given a simultaneous choice test between the familiar bobwhite maternal call A and an unfamiliar bobwhite maternal call (call B). These two calls were recorded in the field (Heaton, Miller, & Goodwin, 1978) and have been shown to be equally attractive to naïve quail chicks (Lickliter & Hellewell, 1992). Testing was conducted in a circular arena (160 cm in diameter), surrounded by a 24 cm wall draped with an opaque black curtain. The floor was painted flat black and the walls surrounding the arena were lined with foam to attenuate the possible sound of echoes. Two rectangular approach areas (32 X 15 cm each) were situated on opposite sides of the arena and demarcated by painted green stripes on the arena floor. These approach areas accounted for less than 5 % of the arena's floor space. A midrange dome-radiator speaker was located behind the curtain in each approach area. These speakers and approach areas were equidistant from the start

point for subjects during testing. Each speaker was connected to a Tascam model 122-B cassette tape recorder.

Once the subject was placed at the start area, the trial began. The speaker in one approach area broadcast bobwhite maternal call A at a peak intensity of 65 dB (A scale, fast response), while the speaker at the opposing approach area broadcast bobwhite maternal call B at the same specifications. A trained observer sat at a table and observed each subject during testing through the use of a large mirror positioned above the arena. A system of stopwatches was used to score latency to approach and duration of response. Latency was scored as the amount of time (in seconds) that elapsed from the onset of the testing trial until the chick entered an approach area. Duration was scored as the cumulative amount of time (in seconds) the subject spent in an approach area during testing. Trials lasted a total of 5 minutes. Chicks that did not approach either approach area received a latency of 300 and duration of 0 seconds for both approach areas, and were scored as a “non-responder.” Chicks that had a duration score that was at least twice as long for one approach area than the other were scored as showing a “preference” for that approach area. Chicks that approached both areas during testing without showing a preference for one were scored as showing “no preference.” In order to assess whether or not activity level was a confounding variable, frequency of approaches to both approach areas was scored using a Fisher Scientific digital counter. Based on previous findings, it was predicted that chicks receiving unimodal auditory stimulation ($n = 24$) or no augmented stimulation ($n = 24$) would prefer the familiar maternal call during testing. It was also predicted that chicks exposed to concurrent prenatal bimodal stimulation ($n = 24$) as embryos would not prefer the familiar call (call A) during testing.

Data Analysis

The primary data of interest in this experiment was preference for one of the auditory stimuli presented during testing. Two such measures were analyzed: (a) differences in the latency of approach to each stimulus and duration spent in each approach area by individual subjects were analyzed with the Wilcoxon matched-pairs signed-ranks test, and (b) an individual preference, derived from the duration measure. Any subject spending twice as long in one approach area than the other was scored as

preferring that stimulus. The distribution of preferences per group was analyzed with the chi-square test. Group differences in frequency of approach to the acoustic stimuli were analyzed with the Kruskal-Wallis test. Alpha-level was set at $p < .05$.

Results and Discussion

The results of Experiment 2 are shown in Tables 2 and 3. Although the concurrent bimodal and control groups showed significantly shorter latencies to approach the familiar call than the unfamiliar call, ($z = -2.343$, $p < .05$; and $z = -2.6$, $p < .01$, respectively), the unimodal auditory group did not demonstrate significant differences in latency to approach the familiar vs unfamiliar call ($z = -1.415$, $p = .157$). The Wilcoxon matched-pairs signed-ranks test on difference in duration of time spent in each approach area was significant for the control group ($z = -3.757$, $p < .001$), the unimodal auditory group ($z = -3.042$, $p < .05$), and the concurrent bimodal group ($z = -4.029$, $p < .001$).

As predicted, the unimodal auditory and control groups showed significant preferences for the familiar bobwhite maternal call (A) at 48 hours of age following exposure for 10 min/hr for the 24 hour period following hatching, $\chi^2(2) = 15.25$; $p < .001$ and $\chi^2(2) = 15.75$; $p < .001$, respectively. Contrary to predictions, the concurrent bimodal group also demonstrated a significant preference for the familiar call, $\chi^2(2) = 27.25$; $p < .001$, with 20 out of 24 subjects demonstrating a preference for the familiar call over the unfamiliar maternal call. A Kruskal-Wallis analysis of variance on frequency of approach was not significant ($\chi^2(2) = 1.84$, $p = .399$), indicating that frequency of approach was not a significant factor in determining group differences on the dependent variables.

Columbus and Lickliter (1997) also found that bobwhite quail chicks demonstrate a significant preference for a familiar call at 48 hours of age following 10 min/hr of exposure during the 24 hour period following hatching. But, similarly to the unimodal auditory group in the present experiment, chicks did not demonstrate significant differences in latency to approach each stimulus. However, it is important to note that subjects from the Columbus and Lickliter study (1997) were not exposed to prenatal sensory stimulation, thus the overall stimulative history of non-control subjects used in the present experiment differed from those in this previous study. The unimodal auditory

group was the only group that did not demonstrate significantly shorter latencies to approach the familiar maternal call than the unfamiliar maternal call. Exposure to moderate amounts of prenatal unimodal visual stimulation has been found to facilitate bobwhite quail chicks' ability to demonstrate postnatal auditory learning under normal rearing conditions (Columbus, 1998). However, prenatal unimodal visual stimulation is associated with slight increases in heart rate and decreased behavioral arousal during exposure (Reynolds & Lickliter, in press), whereas concurrent prenatal bimodal stimulation elicits significant increases in heart rate and behavioral arousal. Based upon these findings, it was predicted that concurrent prenatal bimodal stimulation would interfere with early postnatal auditory learning. Surprisingly, the bimodal exposure group showed the highest proportion of individual preferences for the familiar call. Thus, concurrent prenatal bimodal stimulation appears to affect behavioral arousal in the days following hatching, but it does not appear to interfere with early postnatal auditory learning.

Experiment 3: Effects of Prenatal Sensory Stimulation on Postnatal Responsiveness to Multimodal Maternal Cues

Previous studies have documented a species-typical sequential pattern of postnatal sensory dominance in bobwhite quail. For example, bobwhite quail chicks rely on auditory cues when directing their social preference for bobwhite maternal cues for the initial 48 hour period following hatching. By 72 hours of postnatal age, however, bobwhite quail chicks typically require combined auditory and visual cues in directing their social preferences (Lickliter, 1994; Lickliter & Virkar, 1989; Sleigh, Columbus, & Lickliter, 1998). Thus, under normal developmental conditions there seems to be a transition between 48 to 72 hours of age from a reliance on unimodal auditory cues to the use of multimodal (auditory/visual) maternal cues in directing social preferences. Interestingly, this developmental transition does not depend upon prior exposure to an adult bobwhite hen. In a rather non-obvious manner, social interaction with siblings in the period following hatching appears to play a key role in the transition from reliance on unimodal maternal cues to a reliance on multimodal (auditory/visual) maternal cues in

determining social preferences at 72 hours of postnatal age (Honeycutt & Lickliter, 2001 b; McBride & Lickliter, 1993).

The findings from Experiment 1 indicate that concurrent prenatal bimodal stimulation affects postnatal social behavior in bobwhite quail chicks. Chicks exposed to bimodal stimulation as embryos demonstrated significantly less time huddling with siblings than chicks exposed to unimodal auditory stimulation or no supplemental stimulation in the prenatal period. In addition, the prenatal bimodal exposure group was significantly more active in the open-field when compared to unimodal auditory subjects and controls. The increased behavioral activity level associated with prenatal exposure to bimodal stimulation may interfere with normal patterns of social interaction between broodmates in the days following hatching.

If the utilization of multimodal maternal cues in directing social preferences at 72 hours of age is dependent upon features of social interaction with siblings (Honeycutt & Lickliter, 2001 b), then the effect of concurrent prenatal bimodal stimulation on early postnatal social behavior may serve to interfere with early multimodal maternal responsiveness in bobwhite quail. The purpose of this experiment was to assess the effects of prenatal sensory stimulation on postnatal multimodal maternal responsiveness in bobwhite quail. It was predicted that subjects exposed to concurrent prenatal bimodal stimulation ($n = 24$) would not demonstrate a preference for the bobwhite maternal call paired with bobwhite hen versus a scaled quail hen paired with the bobwhite maternal call at 72 hours of postnatal age. Additionally, it was predicted that chicks exposed to prenatal unimodal auditory stimulation ($n = 24$) and no supplemental stimulation ($n = 24$) as embryos would demonstrate preferences for species-specific bobwhite maternal auditory/visual cues at 72 hours of age, in keeping with the findings of earlier studies (see Lickliter & Banker, 1994).

Method

Following hatching, subjects were reared as described in the General Method section. Subjects were not exposed to any supplemental postnatal stimulation other than that provided by their broodmates. At 72 hours post-hatching, chicks were placed individually in the testing arena (described in more detail in the Method section of

Experiment 2) and provided a simultaneous-choice test. Subjects were presented with a stuffed model of a bobwhite hen in one approach area and a stuffed model of a species-atypical scaled quail hen in the opposing approach area. An identical species-typical auditory cue (bobwhite maternal call B) was broadcast from each approach area. The use of the same maternal call in each approach area required subjects to direct their social preference on the basis of the visual cues provided by the stuffed hen models. Other than the stimuli used in the approach areas, testing and scoring was conducted in the same manner described in the Method Section of Experiment 2.

Results and Discussion

The results of Experiment 3 are shown in Tables 4 and 5. No significant differences in latency to approach each stimulus were found for the control group ($z = -1.045$, $p = .295$), unimodal auditory group ($z = -.713$, $p = .476$), or the concurrent bimodal group ($z = -.228$, $p = .820$). Similarly, no significant differences were found on duration scores for the control group ($z = -1.587$, $p = .113$), unimodal auditory group ($z = -1.4$, $p = .161$), or the concurrent bimodal group ($z = -.517$, $p = .605$). None of the groups demonstrated a significant preference for the bobwhite hen or scaled hen. As predicted the bimodal group demonstrated more no preference scores than preferences for either approach area (see Table 5).

Although no significant within-groups differences were found on the latency and duration scores, a subsequent analysis of the data revealed significant differences between groups on the scaled hen latency and duration measures. A Kruskal-Wallis test on latency to approach the scaled hen approach area was significant, $\chi^2(2) = 8.428$, $p < .05$. The bimodal exposure group ($M = 28.187$) demonstrated shorter latencies to approach the scaled hen area than the unimodal auditory group ($M = 35.85$) and controls ($M = 45.48$). Additionally, a Kruskal-Wallis test on duration of time spent in the scaled hen approach area indicated significant between-group differences, $\chi^2(2) = 6.518$, $p < .05$. The bimodal exposure group ($M = 45.19$) spent greater durations of time in the scaled hen approach area than the unimodal auditory exposure group ($M = 33.42$) and control group (30.90). The bimodal group may have been less able to utilize visual cues during testing than the unimodal auditory and control groups in determining social preferences.

Moreover, the Kruskal-Wallis analysis of variance on frequency of approach revealed significant differences between groups in the present experiment, $\chi^2(2) = 6.589$, $p < .05$. Specifically, the bimodal exposure group ($M = 45.04$) entered the approach areas significantly more often than the unimodal auditory group ($M = 34.5$) and controls ($M = 29.96$). This higher level of activity during testing parallels the results of Experiment 1 (from testing at 24 hours following hatching). The finding that the bimodal exposure group had significantly greater numbers of approaches to the test stimuli during testing at 72 hours of age suggests that concurrent prenatal bimodal stimulation has relatively enduring effects upon the activity levels of bobwhite quail chicks for several days following hatching.

General Discussion

The present study examined the effect of prenatal sensory stimulation on postnatal behavior, perceptual learning, and perceptual responsiveness in bobwhite quail. A number of hypotheses were generated based upon the previous findings related to increased arousal during exposure to prenatal bimodal stimulation and the developmental intersensory interference effect. It was hypothesized that chicks exposed to prenatal bimodal stimulation would demonstrate increased behavioral arousal when compared with chicks exposed to prenatal unimodal auditory stimulation or no supplemental stimulation. A second hypothesis predicted that chicks exposed to prenatal bimodal stimulation would not demonstrate evidence of auditory learning in the days following hatching, while controls and chicks from the unimodal auditory exposure group would demonstrate postnatal auditory learning. A final hypothesis predicted that prenatal bimodal stimulation would interfere with species-typical multimodal maternal responsiveness in bobwhite quail.

Postnatal Behavioral Arousal

Experiment 1 investigated the effects of prenatal sensory stimulation on postnatal behavioral arousal and social behavior in bobwhite quail chicks. As predicted, chicks exposed to concurrent bimodal stimulation as embryos demonstrated greater behavioral activity levels than those exposed to unimodal auditory stimulation or no supplemental stimulation as embryos. Additionally, chicks from the bimodal exposure group huddled with siblings significantly less than control chicks. The increased postnatal behavioral arousal associated with prenatal exposure to bimodal sensory stimulation appeared to influence the chicks' ability to engage in some forms of social behavior with siblings. These findings are significant in that they are the first to demonstrate that concurrent prenatal bimodal stimulation has enduring effects upon the postnatal behavioral organization and social behavior of bobwhite quail.

Postnatal Auditory Learning

Experiment 2 measured the effects of prenatal sensory stimulation on postnatal auditory learning in bobwhite quail chicks. As expected, at 48 hours post-hatching, chicks exposed to prenatal unimodal auditory stimulation or no supplemental prenatal

stimulation demonstrated significant preferences for the familiar bobwhite maternal call as opposed to the unfamiliar bobwhite maternal call. Unexpectedly, chicks exposed to concurrent prenatal bimodal stimulation also demonstrated a significant preference for the familiar bobwhite maternal call. Prenatal exposure to concurrent bimodal stimulation did not appear to have a negative effect upon the capacity of the chicks to discriminate and prefer the familiar call over the unfamiliar maternal call.

These findings appear to support the weak form of the developmental intersensory interference hypothesis, which proposes that concurrent stimulation of immature sensory systems causes a transitory (immediate) interference of selective attention and perceptual learning as opposed to having a long-term impact on an organism's capacity for perceptual learning (Radell & Gottlieb, 1992). The strong form of the developmental intersensory interference hypothesis, proposed by Turkewitz and Kenny (1982, 1985), holds that premature stimulation of the visual system has a permanent impact upon the subsequent development of the auditory system. The premature visual stimulation causes areas of the cortex that would normally be devoted to the auditory system to be allocated to the visual system.

Postnatal Multimodal Maternal Responsiveness

Experiment 3 investigated the effects of prenatal sensory stimulation on the development of responsiveness to species-specific multimodal maternal cues in the days following hatching for bobwhite quail chicks. As predicted, the prenatal bimodal exposure group was unable to demonstrate utilization of multimodal (audio-visual) maternal cues in showing a preference for the bobwhite hen model vs the scaled hen model. In fact, the bimodal exposure group demonstrated shorter latencies to approach and spent greater durations of time in the scaled hen approach area than the unimodal auditory and control groups.

In contrast, the prenatal unimodal auditory exposure group and control group displayed more individual preferences for the bobwhite hen model than the scaled hen model (or no-preference scores). The distribution of preference scores approached (but did not reach) significance for the unimodal auditory and control groups, with both of these groups demonstrating at least twice as many preference scores for the bobwhite hen

model than the scaled hen model. This lack of significance was unexpected based on previous studies from our lab (Lickliter, 1990, 1994; Lickliter & Stoumbos, 1991; Lickliter & Virkar, 1989). The models used in the present study have been used for several years in our lab, perhaps the wear and tear caused by years of aging and testing has affected the visual appearance of the models in a sufficient manner to account for the lack of replication on the preference scores. However, the direction of preferences was as predicted for all groups, with the unimodal auditory and control groups spending greater durations of time in the bobwhite approach area than the scaled hen approach area. The bimodal exposure group did not show this directional trend. Moderate amounts of prenatal unimodal visual or unimodal auditory stimulation have been shown to accelerate the development of species-typical multimodal responsiveness in bobwhite quail (Lickliter, 1990; Sleigh & Lickliter, 1996). The concurrent prenatal bimodal stimulation provided in the present study may have exceeded some range of stimulation optimal for perceptual development provided by the species-typical prenatal environment. Given the tight interconnection between arousal and selective attention in early development (Gardner & Karmel, 1995; Richards & Casey, 1991), it is plausible that the increased levels of postnatal behavioral arousal associated with concurrent prenatal bimodal stimulation may have interfered with the ability of quail chicks' to selectively attend to visual cues in the days following hatching. In other words, the bimodal exposure group may not have been able to differentiate the relevant visual cues provided by each of the stuffed hen models.

Implications for Future Research

Prenatal sensory stimulation was shown to have significant effects upon postnatal behavioral organization and social behavior (Experiment 1). Furthermore, the increased behavioral arousal and decreased display of social behavior associated with prenatal exposure to concurrent bimodal stimulation may have served as a mediator behind the apparent inability of bimodal subjects to utilize species-specific multimodal maternal cues at 72 hours of postnatal age. Chicks exposed to concurrent prenatal bimodal stimulation demonstrated increased activity levels during testing at 24 and 72 hours post-hatching.

One possible reason behind the lack of an effect upon postnatal auditory learning may relate to the amount of prenatal sensory stimulation provided in the present experiment. While subjects in the present study were exposed to 10 min/hr of prenatal sensory stimulation for a six hr period (total exposure time = 60 min), Columbus (1998) found that exposing subjects to 10 min/hr of prenatal visual stimulation for a 24 hr period (total exposure time = 240 min) interfered with postnatal auditory learning under rearing conditions in which unmanipulated control chicks are capable of demonstrating auditory learning. Similarly, 10 min/hr of prenatal exposure to bobwhite hatchling contentment vocalizations during the 24 hr period prior to hatching leads to an acceleration of the emergence of species-typical visual responsiveness (Sleigh & Lickliter, 1996). However, increasing the amount of prenatal exposure to contentment vocalizations to 40 min/hr is associated with an interference with the emergence of species-typical visual responsiveness in bobwhite quail chicks (Sleigh & Lickliter, 1997). Therefore, increasing the total amount of concurrent prenatal bimodal stimulation may lead to deficits in postnatal auditory learning.

Another possible reason behind the lack of an effect upon early postnatal auditory learning may be due to the fact that the auditory system is more fully developed than the visual system of bobwhite quail in the days following hatching. The ability to process unimodal auditory stimulation may require less attentional demands than unimodal visual or multimodal sensory stimulation. A key aspect of the facilitative effects of early social interaction with siblings on multimodal maternal responsiveness is the visual stimulation provided by siblings (Honeycutt & Lickliter, 2001). The increased behavioral arousal demonstrated by the bimodal exposure group may have interfered with their ability to selectively attend to and differentiate the visual information afforded by broodmates that would have fostered development of species-specific perceptual preferences.

On a related note, several studies have shown that timing of exposure is a significant factor in determining how prenatal sensory stimulation may affect an organism's perceptual development (Honeycutt, 2002; Lickliter, 1993; Sleigh & Lickliter, 1998). For example, bobwhite quail chicks exposed to augmented prenatal tactile and vestibular stimulation from day 9 until day 14 of incubation are unable to

demonstrate evidence of prenatal auditory learning of a maternal call at day 22 of incubation during postnatal testing. In contrast, chicks exposed to the same amount of prenatal tactile and vestibular stimulation from day 14 to day 19 of incubation are able to demonstrate evidence of prenatal auditory learning at day 22 of incubation during postnatal testing (Honeycutt, 2002). The auditory system of bobwhite quail becomes functional between day 9 and day 14 of incubation, thus increased levels of tactile and vestibular stimulation at this time may interfere with the early development of the auditory system. The prenatal sensory stimulation in the present experiment was administered during the final 24 hour period prior to hatching, the auditory system is more fully developed than the visual system at this time. Therefore, the timing of exposure may explain the lack of an effect upon the postnatal auditory functioning of the chicks. Future studies should examine the possibility that prenatal concurrent bimodal sensory stimulation (e.g., auditory/vestibular) stimulation may impact postnatal auditory learning if stimulus exposure occurs from day 9 to day 14 of incubation.

A key feature of the prenatal stimulation provided in this study was a lack of synchrony between the amodal properties (e.g., rhythm, rate, intensity) provided by the auditory and visual stimuli. Reynolds, Honeycutt, and Lickliter (2002) found that synchronous bimodal stimulation does not elicit the significant increase in heart rate that is associated with asynchronous bimodal stimulation in the prenatal period. In addition, bobwhite quail embryos presented with a bobwhite maternal call temporally synchronized with patterned light are able to learn the maternal call four times faster than bobwhite quail exposed to unimodal presentation of a maternal call as embryos. In contrast, embryos presented with a maternal call paired with asynchronous patterned light are unable to demonstrate prenatal auditory learning (Lickliter, Bahrack, & Honeycutt, 2002). Taken together, these findings indicate that synchronous, redundant bimodal stimulation has qualitatively different effects upon arousal and perceptual learning in bobwhite quail. Synchronous prenatal bimodal stimulation may evoke arousal levels optimal for perceptual learning. In addition, the intersensory redundancy provided by synchronous bimodal stimulation is likely to provide embryos with a highly salient source of amodal information (Bahrack & Lickliter, 2000; Lickliter, Bahrack, &

Honeycutt, 2002; Reynolds, Honeycutt, & Lickliter, 2002). Thus, prenatal exposure to synchronous bimodal stimulation would be expected to impact postnatal development in a manner dissimilar to asynchronous bimodal stimulation. Future studies should investigate the effects of synchronous vs asynchronous concurrent prenatal bimodal stimulation on postnatal behavioral organization in bobwhite quail. It is likely that chicks exposed to synchronous bimodal stimulation as embryos would not display the increased behavioral arousal and decreased social interaction associated with prenatal exposure to asynchronous bimodal stimulation.

Banker and Lickliter (1993) found that postnatal rearing conditions can lead to a reversal of certain effects of prenatal sensory stimulation on postnatal perceptual responsiveness. Exposure to moderate amounts of prenatal visual stimulation is associated with accelerated development of multimodal (audio-visual) responsiveness in bobwhite quail chicks (Lickliter, 1990). However, chicks exposed to prenatal visual stimulation followed by 24 hours of attenuated postnatal visual stimulation demonstrate normal patterns of multimodal responsiveness (Banker & Lickliter, 1993). Thus, attenuated postnatal sensory stimulation can override the effects of prenatal visual stimulation on postnatal perceptual responsiveness. Whether attenuated sensory stimulation during the early postnatal period would cancel out the effect of prenatal bimodal stimulation on behavioral arousal and social interaction in bobwhite quail is a question worthy of future investigation.

Conclusion

The present study investigated the possibility that the increased behavioral and physiological arousal evoked by prenatal bimodal sensory stimulation may have enduring effects upon the (a) postnatal behavioral organization, (b) perceptual learning, and (c) perceptual responsiveness of bobwhite quail chicks. Exposure to bimodal stimulation in the prenatal period was associated with increased postnatal behavioral arousal and an interference of social behavior for bobwhite quail chicks. Additionally, chicks exposed to prenatal bimodal sensory stimulation were unable to utilize multimodal maternal cues in demonstrating species-specific perceptual preferences. However, there was no effect found for prenatal sensory stimulation on postnatal auditory learning of bobwhite chicks.

The results of this study provide evidence of the impact of an organism's prenatal stimulative history in determining the course of early postnatal perceptual and behavioral development in bobwhite quail. Alterations in the type and/or amount of prenatal sensory stimulation can alter subsequent postnatal activity levels and social behavior, leading to as yet undetermined influences on development in the days and weeks following hatching.

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Table 1: Mean (SD) grid crossings and huddle durations from Experiment 1

<i>Experiment 1</i>	Grid Crossings		Huddle Duration		
	Condition	Mean	SD	Mean	SD
	Control	4.50	3.93	77.00	18.54
	Unimodal Auditory	11.58	11.50	70.67	36.95
	Bimodal	23.25**	17.91	38.83*	13.703

*p < .05
** p < .001

Table 2: Latency and Duration Scores for Experiment 2

<i>Experiment 2</i>	Latency		Duration	
	Condition	Call A	Call B	Call A
Control	16.0	58.0*	105.5	7.5*
Unimodal Auditory	25.5	47.0	65.0	11.0*
Bimodal	18.5	59.0*	86.0	3.5*

Median Scores (in seconds) are shown in table.

*p < .05 (Wilcoxon test)

Table 3: Preference Scores for Subjects in Experiment 2

Experiment 2

Condition	n	n-responding	Preference		
			Call A	Call B	No Preference
Control	24	24	17*	2	5
Unimodal Auditory	24	24	17*	3	4
Bimodal	24	24	20*	1	3

*p < .001 (Chi-Square Test)

Table 4: Latency and Duration Scores for Experiment 3

<i>Experiment 3</i>	Latency		Duration		
	Condition	Bobwhite	Scaled Hen	Bobwhite	Scaled Hen
Control		134.5	254.0	37.5	3.0
Unimodal Auditory		93.5	90.0	36.0	21.0
Bimodal		45.0	37.5	44.0	51.5

Median Scores (in seconds) are shown in table.

Table 5: Preference Scores for Subjects in Experiment 3

<i>Experiment 3</i>			Preference		
Condition	n	n-responding	Bobwhite	Scaled Hen	No Preference
Control	24	20	11	5	4
Unimodal Auditory	24	21	10	5	6
Bimodal	24	24	5	6	13

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Psychological Sciences, Developmental Psychology
Dissertation: Effects of Prenatal Sensory-Evoked Arousal on Postnatal Behavior and
Perceptual Learning in Bobwhite Quail. *Proposal Accepted*
Major Advisor: Robert Lickliter, PhD
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Experimental Psychology
Thesis: Athletic Participation and Gender in Relation to Ego Identity.
Major Advisor: James Perry, PhD
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Psychology

ACADEMIC EMPLOYMENT

- Graduate Teaching/Research Assistant (20 hours) August 2001 – present
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- Lab Manager (20 hours) May 2000 – present
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- Graduate Teaching/Research Assistant (20 hours) January 2000 – May 2000
Virginia Polytechnic Institute and State University, Blacksburg, VA

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Psi Chi Honor Society	East Tennessee State University

AWARDS

NIH Student Travel Award	2000
Virginia Tech Psychology Department Galper Fund Travel Award	2001
NIH Student Travel Award	2001

PROFESSIONAL ORGANIZATIONS

International Society for Developmental Psychobiology

PUBLICATIONS

Reynolds, G.D., & Lickliter, R. (in press). Effects of prenatal sensory stimulation on heart rate and behavioral measures of arousal in bobwhite quail embryos. Developmental Psychobiology.

Reynolds, G.D., Lickliter, R., & Honeycutt, H (in preparation). Effects of redundant and non-redundant bimodal stimulation on heart rate response in bobwhite quail embryos.

Reynolds, G.D., & Perry, J.S. (in preparation). Athletic participation and ego identity.

PRESENTATIONS

Reynolds, G.D., Honeycutt, H., & Lickliter, R. (April, 2002). Effects of redundant and non-redundant bimodal stimulation on heart rate response in quail embryos. Presented at the International Conference on Infant Studies, Toronto, Canada.

Reynolds, G.D., & Lickliter, R. (November, 2001). Effects of intersensory redundancy on physiological arousal in bobwhite quail embryos. Presented at the annual meeting of the International Society for Developmental Psychobiology, San Diego, California.

Reynolds, G.D., & Lickliter, R. (November, 2000). Effects of prenatal sensory stimulation on behavioral arousal in bobwhite quail embryos. Presented at the annual meeting of the International Society for Developmental Psychobiology, New Orleans, Louisiana.

Reynolds, G.D., & Perry, J.S. (March, 2000). Athletic participation and gender in relation to ego identity. Presented at the annual meeting of the Southeastern Psychological Association, New Orleans, Louisiana.

COURSES TAUGHT

Introductory Psychology	2 sections/semester (12 hrs.) East Tennessee State University	August 1998 – May 1999
Introductory Psychology Lab	2 lab sections (2 hrs.) Virginia Polytechnic Institute and State University	August 1999 – December 1999
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