

Type and Amount of Prenatal Auditory Experience Alters
Postnatal Perceptual Responsiveness in Bobwhite Quail

by

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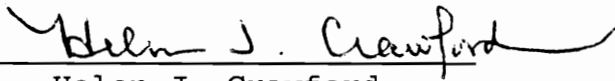
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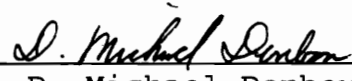
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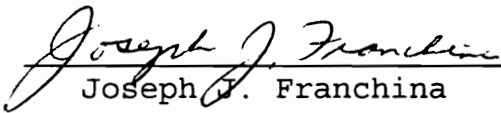
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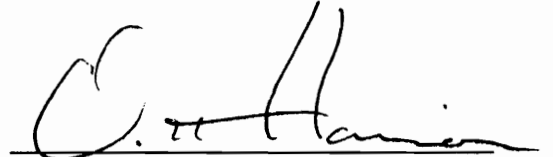
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Robert Lickliter, Chairman

Psychology

(Abstract)

Bobwhite quail embryos were exposed to 5 or 10 min/hr of either bobwhite chick contentment calls or bobwhite chick distress calls. Results revealed that embryos exposed to 5 or 10 min/hr of distress calls continued to respond to maternal auditory cues into later stages of postnatal development in comparison to controls (Experiments 1A & 2A) and failed to demonstrate species-typical responsiveness to maternal visual cues (Experiments 1B & 2B). In contrast, embryos exposed to 5 min/hr of contentment calls continued to respond to maternal auditory cues into later stages of development (Experiment 2A) and exhibited species-typical patterns of visual responsiveness (Experiment 2B). Embryos exposed to 10 min/hr of contentment calls responded to maternal auditory cues into

later stages of postnatal development (Experiment 1A), but showed an accelerated responsiveness to maternal visual cues (Experiment 1B). Behavioral activity measures revealed that augmented auditory stimulation (whether contentment or distress vocalizations) appeared to foster an increase in physical responsiveness when compared to controls (Experiment 3). Taken together, these results suggest that the type and amount of sensory stimulation interact during the prenatal period to influence the course of perceptual development.

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Figure 1. Summary of the Postnatal Preferences of Bobwhite Chicks for Maternal Auditory and Visual Cues Following Normal or Augmented Prenatal Auditory Experience.

Work on the prenatal determinants of intersensory responsiveness in precocial animal infants has demonstrated that modifying sensory experience during the prenatal period can exert important influences on subsequent perceptual organization (Banker & Lickliter, 1993; Gottlieb, Tomlinson & Radell, 1989; Lickliter, 1994; Radell & Gottlieb, 1992). In the most general sense, this body of work demonstrates that the stimulation provided by prenatal conditions, whether typical or atypical, actively shapes the development of subsequent species-specific perceptual capabilities. These demonstrations of the effects of modified sensory experience on subsequent perceptual organization illustrate that normal or usual postnatal perceptual development is a consequence of normal prenatal experience and raise questions about the critical aspects of sensory stimulation that mediate these shifts in early intersensory relationships. For example, results from a number of recent studies suggest that the effect(s) that manipulations of perinatal sensory stimulation might have on early perceptual development is likely to depend on a number of nested factors, including the amount of stimulation provided or denied and the type of sensory

stimulation presented to the young organism. In addition, a number of studies have shown that the organism's response to stimulation depends not only on properties of the stimulus, but also on internal factors associated with the organism itself.

Amount of stimulation

A key factor likely associated with the influence of sensory experience on early perceptual development is the amount of stimulation that the developing organism encounters. T.C. Schneirla (1959, 1965) was a pioneer in articulating the notion that organisms seem to respond to the quantitative aspects of sensory stimulation early in development. Specifically, Schneirla argued that mechanisms governing approach and withdrawal behaviors initially operate in response to the quantitative (i.e., amount or intensity) properties of stimulation, rather than the type or modality of stimulation.

Empirical work has supported Schneirla's notion that young organisms initially respond to the quantitative aspects of sensory stimulation. For example, Lewkowicz and Turkewitz (1980) found that 3-week-old human infants equate auditory and visual inputs on the basis of their intensity,

rather than on the basis of a specific sensory modality. This finding does not hold true for adults. Similarly, non-differential responding to heteromodal stimulation has been shown in neonatal rat pups (Spear & Kucharski, 1984; Spear & Molina, 1987; Spear, Kraemer, Molina, & Smoller, 1988). For example, Spear et al (1988) demonstrated that rat pups (but not adults) can be conditioned to suppress responding to a stimulus in a given modality, then transfer that conditioned suppression to stimuli presented to other modalities.

In a similar vein, the response of bobwhite quail chicks to stimulation present in their rearing environment differs significantly depending on the amount of stimulation provided. Lickliter (1990) demonstrated that altering the amount of input to a later developing sensory system by providing moderate levels of prenatal visual stimulation can accelerate subsequent intersensory functioning. In this study, bobwhite quail embryos were exposed to unusually early visual stimulation, in the form of a pulsing light, for 10 min/hr during the final 24-30 hr prior to hatching. In contrast to the behavior of normally reared chicks, chicks provided prenatal visual stimulation

did not show a preference for a bobwhite maternal call over a chicken call at either 24 hr or 48 hr following hatching. Similar to control chicks, these prenatally manipulated chicks also failed to show a preference when presented with silent visual stimuli in the form of a stuffed bobwhite quail hen and a scaled quail hen. Rather, these chicks required a combination of species-typical auditory and visual stimulation to exhibit a preference for their own species by 24 hr, indicating accelerated intersensory functioning when compared to unmanipulated birds.

Similarly, altering an earlier developing system by providing naturally occurring, but moderately enhanced prenatal auditory stimulation has been found to facilitate species-specific visual responsiveness. Lickliter and Stoumbos (1991) exposed bobwhite quail embryos to 10 min/hr of species-typical auditory stimulation (calls produced by the embryos during the last 24-30 hr of incubation). In other words, the experimental procedure merely increased the amount of naturally occurring auditory stimulation present in the prenatal environment. These chicks exhibited species-typical auditory responsiveness at 12 and 24 hr posthatch. However, these chicks demonstrated

accelerated visual functioning, showing a significant preference for a stuffed bobwhite quail over a stuffed scaled hen (when both were emitting the bobwhite maternal call) by 24 hr of age, several days earlier than unmanipulated control chicks.

Taken together, the results from Lickliter (1990) and Lickliter and Stoumbos (1991) seem to suggest that providing embryos with either moderately enhanced amounts of prenatal auditory or visual stimulation accelerates hatchlings' subsequent use of visual information (in conjunction with auditory cues) to direct preferential responsiveness to maternal cues in the postnatal environment. Several hypotheses have been proposed which might account for these observed changes in preferential behavior as a result of prenatal sensory manipulations. For example, Turkewitz and Kenny (1982, 1985) suggested that sensory limitations during early development both reduce perceptual information and mediate the timing of the introduction of perceptual information, thereby reducing the amount of competition between maturing sensory modalities. In other words, limitations of sensory input during the perinatal period are viewed as a key mechanism

by which the quantity of sensory stimulation available to the young organism is reduced at sensitive stages of perinatal development.

Although Turkewitz and Kenny's (1985) theory does account for some empirical findings in the perceptual development literature, it does not account for all empirical findings. For example, Gottlieb, Tomlinson and Radell (1989) tested Turkewitz and Kenny's hypothesis by exposing mallard duck embryos to concurrent auditory and visual stimulation during the period prior to hatching. Under normal conditions, mallard embryos are able to learn a particular maternal call and demonstrate a preference for that familiar call over an unfamiliar call in a simultaneous auditory choice test following hatching (Gottlieb, 1988). In contrast, embryos receiving visual stimulation concurrently with exposure to the individual mallard maternal call failed to exhibit a preference for that familiar call after hatching. These results appear to support the competition theory proposed by Turkewitz and Kenny, in that premature stimulation of a later developing system (visual) interfered with functioning of an earlier developing system (auditory).

Interestingly, further research revealed that this effect occurred only when embryos were exposed to visual and auditory stimulation concurrently. Embryos provided non-concurrent visual stimulation and exposure to the individual maternal call demonstrated a preference for the familiar call over an unfamiliar maternal call in a simultaneous auditory choice test following hatching (Gottlieb et al, 1989). This finding stands in contrast to the results that would be predicted according to Turkewitz and Kenny (1985), in that early visual stimulation did not lead to lasting deficits in auditory learning under all conditions. In other words, intersensory interference was not permanent and occurred only when two competing stimuli were presented concurrently.

Taken together, these findings led Gottlieb and his colleagues (1989) to suggest that concurrent stimulation may compete for the embryo's attention, with an excessive amount of stimulation overloading the organism's attentional capabilities. To explore this hypothesis, Radell and Gottlieb (1992) manipulated the amount of prenatal vestibular stimulation experienced by mallard embryos. Embryos were placed on a waterbed, which was pulsed with waves for the last 24 hr prior to hatching and the 24 hr after hatching. The wave pulses lasted 45 min

each, with 40 min rest periods in between bouts of stimulation. During the waterbed stimulation, embryos were exposed to an individual maternal mallard call. In a simultaneous auditory choice test following hatching, these ducklings failed to show a preference for the familiar call over an unfamiliar mallard call. In other words, concurrent vestibular and auditory stimulation disrupted prenatal auditory learning. A subsequent experiment revealed that non-concurrent waterbed stimulation and exposure to an individual maternal call did not interfere with the embryo's ability to learn the familiar call. Radell and Gottlieb (1992) next exposed embryos to a reduced amount of waterbed stimulation, which more closely approximated their normal range of prenatal vestibular stimulation, and a concurrent maternal call. Interestingly, these ducklings demonstrated a postnatal preference for the familiar call. Thus, when the amount of vestibular stimulation provided was attenuated towards more typical levels, it did not interfere with prenatal auditory learning.

These findings suggest the possibility that intersensory interference occurs only when stimulation to immature sensory systems exceeds a certain level or threshold. Radell and Gottlieb (1992) suggest that the

amount of stimulation an organism encounters in its typical developmental context may be optimal for its species-specific perceptual development. In other words, sensory experience that falls within a range of stimulation typical for that species should not interfere with intersensory development, and mildly enhanced levels of stimulation may maintain or even facilitate typical perceptual development. This hypothesis would potentially explain the findings of Lickliter (1990) and Lickliter and Stoumbos (1991), in which enhanced prenatal visual or auditory stimulation led to accelerated intersensory functioning. If some optimal range of prenatal stimulation exists, then stimulation that falls short of or exceeds that optimal range should cause interference in intersensory functioning, as reported in the Gottlieb et al (1989) and Radell and Gottlieb (1992) studies.

In light of this notion of organisms' differential responsiveness to varied amounts of stimulation, recent work seems to lend support to the existence of some optimal range of perinatal stimulation necessary for species-typical perceptual development. For example, Lickliter and Hellewell (1992) demonstrated that the ability of bobwhite quail to learn a particular call prenatally is dependent upon the amount of stimulation to which they are exposed.

Quail embryos exposed to a variant of a bobwhite maternal call (Call B) show a preference for that call over a different bobwhite maternal call (Call A) 24 hr after hatching. However, embryos exposed to Call B and 10 min/hr of patterned light concurrently failed to demonstrate a preference for Call B. In contrast, when provided with the light and Call B non-concurrently, hatchlings did prefer the familiar call B, demonstrating their ability to learn this call prenatally and indicating that concurrent stimulation, in this situation, interferes with prenatal auditory learning.

In the same study, this effect was also demonstrated postnatally. Quails exposed to Call B in a postnatal social setting with same-age chicks did not exhibit a preference for that call. In contrast, quails exposed to the same call postnatally in social isolation did prefer familiar Call B. These findings suggest that the greater amount of overall stimulation provided by social rearing interfered with postnatal auditory learning, while a more moderate level of stimulation provided by social isolation facilitated learning the individual maternal call. These findings parallel those of Radell and Gottlieb (1992), in that when overall amounts of stimulation exceeded a certain level, a negative impact on early auditory learning was

observed.

In a similar vein, Krutchkoff and Lickliter (in preparation) recently provided quail embryos with levels of vestibular stimulation that greatly exceeded those experienced under normal incubation conditions by rotating incubating eggs in a circular pattern for 7 min/hr throughout the last week of incubation. The direction of the rotation alternated each hour, with the eggs rotating in a clockwise fashion during one hour, and then rotating counter-clockwise in the following hour. This increased vestibular stimulation interfered with subsequent species-typical auditory and visual responsiveness to maternal cues. In other words, increasing the amount of prenatal stimulation to an earlier developing modality (vestibular) interfered with the development of later developing modalities (auditory and visual).

Substantially increasing the amount of stimulation to a later developing system also seems to interfere with intersensory functioning. For example, Sleigh and Lickliter (1995) exposed bobwhite quail embryos to 40 min/hr of patterned visual stimulation during the last 24 to 30 hr prior to hatching. This substantially increased amount of prenatal visual stimulation interfered with subsequent species-typical auditory and visual

responsiveness to maternal cues. Specifically, chicks in this study continued to respond to maternal auditory cues into later stages of postnatal development and failed to respond to maternal visual cues at the age when normally reared chicks exhibit this species-specific ability. Recall that Lickliter (1990) demonstrated that embryos exposed to 10 min/hr of prenatal visual stimulation show accelerated intersensory functioning during the days following hatching. Taken together, the results from Sleigh and Lickliter (1995) and Lickliter (1990) provide further evidence that moderate amounts of stimulation appear to facilitate species-typical functioning, whereas substantially augmented amounts of stimulation appear to interfere with species-typical functioning.

In a similar vein, Kenny and Turkewitz (1986) provided rat pups with unusually early visual experience by surgically opening their eyelids approximately 10-12 days prior to the typical period for eyelid opening. As a result of this early visual experience, rat pups continued to exhibit homing behaviors beyond the time at which unmanipulated pups ceased to show the same behavior. When visual cues were removed, the early eye-lid opened pups behaved similar to normal pups, suggesting that the eye opening procedure resulted in earlier functioning of the

visual system. This increase in the amount of stimulation to the visual system appeared to interfere with species-typical intersensory development by creating a reliance on visual cues instead of the normal utilization of olfactory cues at this age of development.

Whereas significantly augmented stimulation may interfere with subsequent perceptual functioning, a decrease in the overall levels of sensory stimulation can also interfere with normal patterns of perceptual organization. Gottlieb (1993) examined the impact of postnatal physical isolation rearing on ducklings' ability to learn a species-atypical chicken call. Previous research has demonstrated that socially-reared ducklings exposed to an individual chicken call for the 48 hr prior to and 48 hr after hatching can learn and show a preference for that familiar chicken maternal call over an unfamiliar mallard maternal call (Gottlieb, 1991b). In contrast, ducklings undergoing the same procedure, but reared in conditions of postnatal isolation where they could see broodmates (but could not make physical contact with them) did not learn the chicken maternal call. Similarly, ducklings reared in postnatal individual isolation, where they could neither see or touch broodmates, did not learn the chicken maternal call. The results of these two

experiments indicate an interference in auditory learning as a result of attenuated postnatal tactile stimulation. Recall that Lickliter and Hellewell (1992) demonstrated that bobwhite quails reared in postnatal social isolation did exhibit the ability to learn an individual species-typical maternal call. These conflicting results may be explained by the differential difficulty of the tasks. Gottlieb (1991b) required ducklings to learn a species-atypical maternal call, whereas Lickliter and Hellewell (1992) exposed the bobwhite quail to a species-typical maternal call. This finding suggests that the level of stimulation that is optimal for learning may shift as a function of task complexity.

In a subsequent experiment, Gottlieb (1993) reared individual ducklings with inanimate stuffed ducklings. Under these conditions the individual hatchling could make physical contact with and see duckling replicas, but could not interact with live broodmates. Interestingly, these ducklings did learn and prefer the familiar chicken call. Taken together, these experiments seem to suggest that attenuated amounts of postnatal tactile stimulation resulting from physical isolation from broodmates can interfere with typical patterns of postnatal auditory

learning, while amounts of tactile stimulation that fall within a more typical range maintain normal patterns of auditory learning.

Lickliter and Lewkowicz (1995) recently examined the impact of prenatal physical isolation and the consequent altered levels of sensory stimulation on bobwhite quail embryos' and hatchlings' perceptual functioning. Quail embryos were incubated in physical isolation during the final 24 to 30 hr prior to hatching. During this social isolation, embryos could hear other embryos in the incubator but could not physically contact these embryos. Embryos were then provided either no prenatal visual stimulation or 10 min/hr of patterned visual stimulation. Following hatching, birds in both groups preferred the bobwhite maternal call at 24, 48, and 72 hr and did not demonstrate a preference for maternal visual cues at any age tested. These findings stand in contrast to communally incubated chicks, who rely on auditory stimuli for the first two days after hatch, and then require both auditory and visual cues at 72 hr to direct their social preferences (Lickliter & Virkar, 1989). Additionally, these findings stand in contrast to chicks which received 10 min/hr of prenatal visual stimulation in a social setting and subsequently preferred the bobwhite hen over the scaled hen

by 24 hr of age (Lickliter, 1990).

In the same study, embryos were incubated in physical isolation while being exposed to an individual maternal call for 10 min/hr during the last 24 to 30 hr prior to hatching. These birds failed to show a preference for the familiar maternal call at 24 hr following hatching. This result stands in contrast to communally incubated chicks, who demonstrate prenatal auditory learning (Lickliter & Hellewell, 1992). To explore what effect the attenuated sensory stimulation caused by physical isolation during incubation had on these results, a second group of embryos was incubated in isolation and received exposure to an individual maternal call with concurrent visual stimulation. These birds did display a preference for the familiar call, indicating that increasing the amount of overall stimulation provided the embryos during exposure to the maternal call resulted in prenatal auditory learning. Interestingly, communally incubated embryos in a previous study that had received visual stimulation concurrently with an individual call did not show a preference for that familiar maternal call in subsequent testing (Lickliter & Hellewell, 1992). Taken together, these results indicate that substantially increased or substantially decreased levels of prenatal stimulation can interfere with early

auditory learning.

Thus, the amount of stimulation present, whether from naturally occurring or experimentally provided sources, appears to have significant impact on prenatal and postnatal perceptual functioning. Specifically, it has been argued that the amount of stimulation provided by either the prenatal or early postnatal environment can serve to either increase or decrease sensitivity to specific auditory or visual stimulation present in that environment (Gottlieb, 1991b, 1993). Stimulation that falls within some optimal range seems to maintain or facilitate normal patterns of perceptual functioning (Lickliter, 1990; Lickliter & Stoumbos, 1991). On the other hand, augmented or attenuated stimulation appears to interfere with normal patterns of perceptual functioning (Gottlieb, 1993; Krutchkoff & Lickliter, in preparation; Lickliter & Lewkowicz, 1995; Radell & Gottlieb, 1992).

Type of stimulation

In addition to amount of stimulation, the effects of sensory stimulation on subsequent perceptual organization may also be influenced by the specific type of stimulation to which the developing organism is exposed. For example, Sleigh, Columbus and Lickliter (in press) incubated bobwhite embryos in either communal or isolation conditions

and provided exposure to either bobwhite chick contentment calls or bobwhite chick distress calls. Results revealed that socially incubated embryos could learn an individual bobwhite maternal call, whereas embryos denied physical and tactile stimulation as a result of isolation incubation failed to demonstrate prenatal auditory learning of the maternal call. In contrast, embryos exposed to contentment calls in the period prior to hatching demonstrated prenatal auditory learning, whether they were incubated socially or in isolation. Socially and isolation incubated embryos exposed to the bobwhite distress calls failed to learn the individual maternal call, indicating that the type of sensory stimulation that the developing organism encounters prenatally is important in fostering normal perceptual development.

In a similar vein, Lickliter and Stoumbos (1991) found that only certain types of enhanced prenatal auditory stimulation serve to facilitate chicks' species-specific visual responsiveness. Specifically, when bobwhite quail embryos were exposed to increased amounts of vocalizations that typically occur in the late prenatal environment, postnatal visual functioning was accelerated. In other words, chicks exhibited a preference for a species-typical stuffed bobwhite hen over a species-atypical stuffed scaled

hen (when both hens emitted the bobwhite maternal call) in a simultaneous choice test following hatching. In contrast, bobwhite quail embryos exposed to bobwhite embryonic vocalizations with a faster repetition rate than normal did not show this accelerated pattern of postnatal visual responsiveness (Lickliter & Stoumbos, 1991), indicating that type of stimulation can be an important variable in understanding how sensory experience mediates subsequent perceptual functioning. Interestingly, this finding raises the possibility that type may serve a mediating role in determining what constitutes an optimal amount of stimulation. In other words, the level of stimulation needed to maintain or facilitate species-typical development may depend, at least to some extent, on the type of sensory stimulation the embryo encounters during the prenatal period.

The type of sensory stimulation encountered during the prenatal period also appears to have a significant impact on the type of stimulation chicks subsequently prefer in the postnatal environment. McBride and Lickliter (1995) recently demonstrated that bobwhite quail chicks exposed to particular auditory stimulation prenatally exhibit a strong preference for those familiar auditory cues when tested postnatally. In one experiment, embryos were exposed to

bobwhite vocalizations with a faster repetition rate. Recall that chicks exposed to bobwhite vocalizations with a faster repetition rate in the Lickliter and Stoumbos (1991) study did not demonstrate accelerated species-typical perceptual responsiveness in subsequent postnatal choice tests. Interestingly, chicks in the McBride and Lickliter (1995) study did exhibit this accelerated responsiveness, but only when the auditory cues employed in postnatal testing also had an increased repetition rate. These findings suggest that the type of auditory stimulation experienced during the prenatal period directs chicks' preferential responsiveness during the postnatal period. Specifically, chicks appear to prefer postnatal auditory stimulation that is similar to their prenatal auditory experience. This preference for the familiar has been demonstrated across many species. For example, DeCasper and Spence (1986) asked pregnant mothers to read to their unborn infants. Following birth, infants exhibited a preference for recordings of the familiar stories over unfamiliar stories. In a similar vein, rat pups exposed to a particular taste in utero subsequently prefer that familiar taste over an unfamiliar taste when tested postnatally (Smotherman, 1982).

This notion that type of stimulation experienced

prenatally directs postnatal preferential responsiveness also appears to be the case with mallard ducklings. Under normally occurring conditions, duck embryos show discriminative responses to species-typical mallard maternal calls (Gottlieb, 1971). In an effort to determine susceptibility to the influence of a species-atypical maternal call, Gottlieb (1991a) exposed three groups of socially-isolated ducklings to a species-atypical chicken maternal call from day 24 of embryonic development to 48 hr following hatching. One group of ducklings was muted, a second group had intact voices, and a third group had intact voices and was also exposed to the recording of a duck embryo contact call. Only the ducklings reared in social isolation and muted preferred the familiar maternal chicken call over a species-typical mallard maternal call in a subsequent simultaneous auditory choice test. These results suggest that mallard ducklings demonstrate auditory learning of a species-atypical call only when they are not able to hear their own voices.

In a subsequent experiment, Gottlieb (1991b) exposed ducklings to a species-atypical chicken maternal call from day 24 of embryonic development to 48 hr following hatching. When the ducklings were reared in social isolation, they failed to demonstrate auditory learning

ability of this species-atypical call. In contrast, ducklings reared socially did demonstrate this ability. Interestingly, the socially reared ducklings demonstrated this ability only when exposure to the chicken call occurred both prenatally and postnatally. Ducklings exposed to the chicken call only prior to hatching or only following hatching failed to show a preference for the familiar chicken call. The culmination of these experiments suggest that auditory learning of a species-atypical maternal call is a more difficult task for the young organism than is auditory learning of a species-typical maternal call. In other words, the type of stimulation employed mediates the particular parameters in which auditory learning can occur.

Just as the type of stimulation encountered prenatally can impact perceptual organization, the type of stimulation encountered postnatally can also influence this organization. For example, McBride and Lickliter (1994) exposed bobwhite quail hatchlings to augmented amounts of bobwhite chick distress calls, bobwhite chick contentment calls, or domestic chicken distress calls during the first 72 hr following hatching. Bobwhite hatchlings exposed to either the bobwhite chick contentment calls or the domestic chicken hatchling distress calls demonstrated species-

typical auditory and visual responsiveness to maternal cues at 72 hr following hatching. In contrast, bobwhite hatchlings exposed to bobwhite chick distress calls did not exhibit species-typical visual responsiveness to maternal cues, suggesting that specific types of auditory stimulation can differentially impact early postnatal intersensory functioning. Specifically, the results of this study suggest that type of sensory stimulation present in the postnatal environment may be a more important factor in subsequent perceptual development than is amount of stimulation. What remains to be explored is if this relationship between type of stimulation and amount of stimulation is also present in the prenatal period of development.

Organismic characteristics

A third factor that potentially mediates the influence of sensory experience on early perceptual development is the experiential history and developmental state of the organism at the time the stimulation is presented or denied. Consistent with a viewpoint advocated by Schneirla (1959, 1965) and Kuo (1967), the organism's response to stimulation has been found to depend not only on the physical aspects of the stimulus, but also on the factors associated with the organism itself. For example, the

arousal level, the experiential history, and the developmental condition of an organism can serve to mediate the influence of any given sensory stimulation on perceptual responsiveness. In this light, Karmel, Gardner, and Magnano (1991) suggested that, for the neonate, perceptual capability is simultaneously determined by both internal and external stimulation. In other words, arousal and attention are inextricably intertwined in early development. Karmel et al (1991) argue that infants do not passively respond to specific stimulus features, but rather the "attentional value" of a stimulus can be modified by either altering the infant's overall arousal level or by altering the nature of sensory experience, regardless of modality.

From this view, any given stimulus can be considered on the basis of at least two measures. The first measure of a stimulus is its "objective" intensity and the second is its "effective" intensity. The objective intensity of a stimulus is the quantitative (physical) measure of intensity. On the other hand, the effective intensity of a stimulus is the intensity actually perceived by the organism. In other words, it is the relationship between the organism and the stimulus that determines the effective intensity of the stimulus. Consequently, to measure the

effective intensity of a given stimulus, the context in which it is presented must be explored, as well as the state and developmental history of the organism.

Gray (1990) recently proposed a similar hypothesis based on his work with domestic chicks. He argued that responsiveness to experimental manipulations is mediated by the arousal level of the organism. Gray's work is based in part on the Yerkes-Dodson law, which argues a curvilinear relation between arousal and performance (Yerkes & Dodson, 1908). Excessive or reduced arousal levels are generally associated with poor performance, while moderate levels of arousal are associated with peak performance. In other words, amount of external stimulation may impact an organism's arousal level and thereby serve to increase or decrease the embryo or infant's sensitivity to specific sensory stimulation present in the perinatal environment.

One effort towards uncovering how the amount of stimulation to which an organism is exposed alters sensitivity to environmental conditions has been provided by work with human infants. Lewkowicz and Turkewitz (1980) demonstrated that prestimulating an infant with a pulse of white noise resulted in infants' increased looking at a dimmer light and decreased looking at a brighter light in comparison to unstimulated infants. In a subsequent

experiment, infants exposed to auditory stimulation immediately preceding or presented concurrently with visual stimuli preferred the less intense visual stimulation (Lewkowicz & Turkewitz, 1981). Similar results were found by Gardner, Lewkowicz, Rose and Karmel (1986) using either auditory or visual stimulation prior to testing. Taken together, these findings suggest that changing the arousal level of infants through visual or auditory prestimulation alters their subsequent visual stimulation preference.

Although organismic characteristics serve to mediate the influence of any given stimuli, these characteristics are often ignored by researchers. Studies focusing on early development tend to take behavioral measures at a single point in time and neglect the ongoing and real time "experience of experience" (but see King & West, 1987; McBride & Lickliter, 1994). A useful measure for uncovering the state of the organism at the time stimulation is presented or denied is multiple observations of the organism's behavior throughout the relevant time period. Efforts to this end could potentially unpack the relationship between how an organism behaviorally responds to particular stimulation and how that behavior serves to impact the organism's subsequent perceptual responsiveness.

In sum, the effect that a manipulation of sensory

experience may have on perinatal perceptual development is likely to depend on a number of interrelated factors, including the amount of stimulation provided, the type of stimulation provided, and features of the organism itself. As a first step in examining the nested relationship between these factors during the prenatal period, this dissertation assessed the effects of different amounts of two unique types of species-typical prenatal auditory stimulation on the development of species-specific auditory and visual responsiveness in bobwhite quail chicks. In addition, the present study was designed to explore whether the range of stimulation that appears optimal for normal perceptual organization shifts as a consequence of the type of stimulation presented. To this end, bobwhite quail embryos were exposed to differing amounts of either bobwhite hatchling contentment calls or bobwhite hatchling distress calls during the final 24 to 30 hr prior to hatching and their subsequent postnatal perceptual preferences for maternal auditory and visual cues was assessed. I hypothesized that exposure to bobwhite distress calls would interfere with species-typical patterns of perceptual development, while exposure to bobwhite contentment calls would maintain or facilitate species-typical patterns of development. In addition, the

present study included multiple visual and auditory observations of embryos in each stimulation condition during baseline periods and during exposure to auditory stimulation in an attempt to assess the presence of behavioral states that may be associated with particular stimulation and may contribute to subjects' behavior during the subsequent postnatal testing trials. I hypothesized that embryos exposed to bobwhite distress calls would have more behavioral activity, indicating increased arousal levels as a result of exposure to that particular type of stimulation.

General Methods

Certain features of the experimental design were common to all experiments, so these features are described first before presenting the particular details of each experiment.

Subjects

Subjects were 528 maternally naive, incubator-reared bobwhite quail embryos (Colinus virginianus). Fertile, unincubated eggs were received weekly from a commercial supplier and were set in a Petersime Model I incubator, maintained at 37.5 degrees Celsius and 85% humidity. After 20 days of incubation, the eggs were transferred to a hatching tray located in the bottom of the incubator

(bobwhite quail typically hatch between Day 22 and Day 23). Only those birds that hatched during Day 23 were used as subjects to control for possible effects of variations in developmental age. The embryo's age is calculated on the basis of the first day of incubation being Day 0, the second 24 hr of incubation being Day 1, and so on. The possible influence of between-batch variation in behavior was controlled by drawing subjects for each experimental group from three or more different batches (i.e., weeks) of eggs. After hatching, subjects were reared in groups of 10 to 12 same-age chicks to mimic naturally occurring brood conditions. As a result of their incubation rearing, the only sounds to which chick embryos and hatchlings were exposed until the time of experimental manipulation or testing was their own embryonic and postnatal vocalizations (and those of their broodmates) and the low-frequency background noises emanating from the incubator fan and motor. The sound-attenuated room in which the hatchlings were reared is illuminated by a 100-W brooder lamp suspended above plastic rearing tubs, which maintained an ambient air temperature of approximately 30 degrees Celsius.

Procedure

To ensure that the embryos were able to hear the

enhanced auditory stimulation, during the second half of the 21st day of incubation, a portion of the shell and the inner shell membrane over the air space of the egg of each subject were removed. The embryo's bill usually penetrates the air space of the large end of the egg early on Day 21 and at this time the embryos begins to respire and vocalize (Freeman & Vince, 1974). As a result, removing a small portion of the shell does not affect postural orientation, incubation, survivability, or species-typical perceptual behavior (Banker & Lickliter, 1993; Lickliter, 1990). Following the egg opening procedure, opened eggs were placed in a portable, Hovi-bator incubator. Temperature and humidity were maintained as during earlier incubation.

Embryos were stimulated with either bobwhite distress vocalizations or bobwhite contentment vocalizations for either 10 min each hours during the last 24 hr prior to hatching (total exposure time = approximately 240 min) or for 5 min each hour during the last 24 hr prior to hatching (total exposure time = 120 min). The recording of bobwhite chick distress calls was obtained during the course of observations of isolate-reared bobwhite hatchlings in a previous study (McBride & Lickliter, 1993; see Stoumbos & Lickliter, 1990 for acoustical details). The recording of the bobwhite chick contentment calls was obtained during

the course of observations of normally reared bobwhite hatchlings (see Stoumbos & Lickliter, 1990 for acoustical details). The bobwhite chick calls were broadcast via a Marantz PMD 221 cassette tape recorder at a uniform peak intensity (65 dB), measured by a sound-level meter.

Testing

Testing occurred at 24 hr, 72 hr, or 96 hr (+/- 3 hr) after hatching. Testing occurred in a circular arena, 160 cm in diameter, surrounded by a wall 24 cm in height and draped by an opaque black curtain to shield the observer from the subject's view. The walls of the apparatus were lined with foam to attenuate echoes, and the floor was painted flat black. Two rectangular approach areas (32 X 15 cm) were demarcated on opposite sides of the arena by green strips painted on the floor. These approach areas made up less than 5% of the total area of the arena. A midrange dome-radiator speaker was positioned behind the curtain in each of the approach areas, equidistant from the point at which each subject was placed in the apparatus. Each speaker was connected to a Tascam model 122-B cassette tape recorder located on a control table. The observer, drawn from trained undergraduates blind to the experimental design, sat at this table and observed each subject's activities through a large mirror positioned above the

arena. A system of stop watches was used to score latency and duration of response, as described below.

During testing, each quail chick was placed singly in the test apparatus equidistant from the two approach areas. During the 5-min test, subjects were scored on both latency of approach and duration of time spent in each of the two approach areas. In the simultaneous-choice test, the locations of the stimuli presented was alternated between subjects to prevent any possible side bias from influencing results. Each subject was tested only once, and latency was scored as the amount of time (in seconds) that elapsed from the onset of the trial until the bird entered an approach area. Duration was scored as the cumulative amount of time (in seconds) the subject remained in an approach area during the 5-min test. A chick that did not enter either approach area received a score of 300s latency (the length of the trial) and 0s for duration for that stimulus and was considered a "non-responder". A chick that stayed less than 10 sec in each approach area was also scored as a "non-responder" to avoid scoring random movement as a behavioral preference. A chick that stayed in one approach area for more than twice the time it spent in the opposing approach area over the course of the 5-min trial was scored with a preference for that stimulus. A

chick that approached both approach areas during a test without showing a preference for either one was scored as "no preference." This measure of preference yielded a convenient summary of the behavior of each bird in the various groups (see Appendix A for a sample rating sheet).

Data Analysis

Before performing any statistical analyses, testing duration scores of less than 10 seconds were replaced with a score of zero, to avoid scoring accidental responses as subjects moved about the arena. The corresponding latency score was replaced with a score of 300s (the length of the testing trial). The primary data of interest were measures of preference for the auditory and visual stimuli presented during the trials. Two such measures of preference were analyzed: (a) differences in the latency of approach to each stimulus by a subject in a group was evaluated by the Wilcoxon matched-pairs signed-ranks test, and (b) an individual preference, derived from duration of response and assigned to any subject that stayed in one area for more than twice as long as the other approach area, was evaluated by a chi-square test. Significance levels of $p < .05$ were used to evaluate results.

Experiment 1A: Effects of 10 Min/Hr of Prenatal Exposure to Bobwhite Contentment Calls or Bobwhite Distress Calls on Postnatal Auditory Responsiveness

As previously discussed, McBride and Lickliter (1994) demonstrated that bobwhite chicks respond differentially to hatchling contentment calls versus hatchling distress calls when the calls are presented in the days immediately following hatching. Specifically, augmented postnatal exposure to the distress call led to deficits in chicks' normal patterns of perceptual functioning. The influence of type of stimulation may be even more powerful during the prenatal period, when the emerging sensory systems are becoming functional.

During the late stages of the prenatal period, quail embryos' vocalizations typically consist of infrequent contentment vocalizations (Sleigh, 1994; Stoumbos & Lickliter, 1990). In contrast, embryos do not typically emit or experience bobwhite hatchling distress calls during this time. Thus, one type of auditory stimulation employed in the present study is typically present in the embryos' prenatal environment (contentment vocalizations), whereas the other type of auditory stimulation employed is typically rare or absent in the embryos' prenatal environment (distress vocalizations). Recall that

Lickliter and Stoumbos (1991) were able to accelerate species-typical perceptual development by providing embryos with augmented amounts of naturally occurring embryonic vocalizations in the days prior to hatching. Thus, birds prenatally exposed to 10 min/hr of bobwhite hatchling contentment calls are expected to demonstrate a preference for the bobwhite maternal call over a species-atypical maternal call at 24 hr of age as seen in the Lickliter and Stoumbos (1991) study.

If the amount of stimulation overrides the type of stimulation provided, then bobwhite quail embryos exposed to 10 min/hr of bobwhite hatchling distress calls during the final 24 hr prior to hatching should appear similar to embryos exposed to 10 min/hr of bobwhite chick contentment vocalizations. Specifically, these subjects should demonstrate accelerated visual responsiveness to maternal cues (as predicted by the results of Lickliter & Stoumbos, 1991). If the amount of stimulation which falls within some optimal range for species-typical development is mediated by the type of stimulation, then bobwhite quail embryos exposed to 10 min/hr of bobwhite distress calls during the period prior to hatching should demonstrate altered species-typical patterns of perceptual development when compared to embryos exposed to 10 min/hr of bobwhite

contentment calls. These results would be expected if bobwhite distress vocalizations are aversive to embryos, as they appear to be to hatchlings (McBride & Lickliter, 1994).

Methods

120 bobwhite quail embryos, drawn from eighteen separate hatches, served as subjects. The shell and membrane over the air space of the egg of each subject were removed as described in the General Methods section. After this procedure, subjects were incubated in groups of 10 to 12 same-aged embryos. Subjects were stimulated for 10 min per hour for a minimum of 24 hr from the second half of Day 21 to the second half of Day 22 of incubation. Sixty embryos were exposed to recorded bobwhite hatchling contentment vocalizations (see Stoumbos & Lickliter, 1990 for acoustical details). A second group of sixty embryos was exposed to bobwhite hatchling distress vocalizations (characterized by long note duration and high pitch, see Stoumbos & Lickliter, 1990 for acoustical details). To determine if either of these prenatal manipulations affected hatchlings' species-typical auditory preference for the maternal call, subjects in each condition were given a simultaneous-choice test between a bobwhite maternal call and a chicken maternal call (see General

Method) at either 24 hr (n = 20 from contentment call group and n = 20 from distress call group), 72 hr (n = 20 from contentment call group and n = 20 from distress call group) or 96 hr (n = 20 from contentment call group and n = 20 from distress call group) following hatching. During testing, the calls were broadcast at a uniform peak intensity (65 dB, B-weighted scale, fast response), measured by a sound-level meter at the point where the chick was introduced into the arena. Acoustical details of the calls are provided by Heaton et al (1978) and Gottlieb (1971). Choice, latency, and duration measures were scored as described in General Methods.

Results and Discussion

Results are shown in Tables 3 and 4. Chicks exposed to 10 min/hr of either bobwhite chick distress calls or bobwhite chick contentment calls demonstrated a significant preference for the species-specific bobwhite maternal call over a chicken maternal call at all ages tested ($p < .01$ in all cases). Chi-square values for the birds exposed to bobwhite contentment calls were as follows: 24 hrs = 38, 72 hrs = 18.46, and 96 hrs = 15.38. Chi-square values for the birds exposed to bobwhite distress calls were as follows: 24 hrs = 40, 72 hrs = 28, and 96 hrs = 26 (degrees of freedom = 2 in all cases). Analysis of latency

and duration scores supported these results, with chicks showing significantly shorter latencies and longer duration in their response to the bobwhite maternal call than to the species-atypical chicken maternal call ($p < .01$ in all cases).

These findings stand in contrast to results obtained from unmanipulated chicks in previous experiments (Lickliter, 1994; Lickliter & Virkar, 1989). Specifically, unmanipulated chicks show a naive auditory preference for the bobwhite maternal call over a species-atypical maternal call at both 24 and 48 hr following hatching, but require combined maternal auditory and maternal visual cues to direct social preferences by 72 hr following hatching (see Table 1). In the present experiment, chicks exposed to 10 min/hr of either bobwhite chick distress calls or bobwhite chick contentment calls continued to demonstrate a preference for the bobwhite maternal call at 96 hr following hatching, indicating a deceleration in the emergence of species-typical patterns of intersensory functioning.

The purpose of the next experiment was to investigate whether the effects of prenatal exposure to bobwhite contentment calls generalizes to responsiveness in other sensory systems by examining the effect of this prenatal

exposure on chicks' postnatal visual, rather than auditory, responsiveness to maternal cues. Based on the results of Lickliter and Stoumbos (1991), chicks exposed to 10 min/hr of bobwhite contentment calls were expected to demonstrate a preference for species-typical maternal visual cues over species-atypical maternal visual cues by 24 hr of age.

This pattern of responsiveness would indicate accelerated species-typical perceptual development. In contrast, chicks exposed to 10 min/hr of bobwhite distress calls were expected to exhibit deficits in species-typical patterns of development, indicating that type of stimulation is indeed a mediating factor in perceptual outcome.

Experiment 1B: Effects of 10 Min/Hr of Prenatal Exposure to Bobwhite Contentment Calls or Bobwhite Distress Calls on Postnatal Auditory/Visual Responsiveness

Methods

120 bobwhite quail embryos, drawn from fifteen separate hatches, underwent the same procedure as subjects in the previous experiment. Subjects were tested at either 24 hr (n = 20 from contentment call group and n = 20 from distress call group), 48 hr (n = 20 from contentment call group), 72 hr (n = 20 from distress call group and n = 20 from contentment call group), or 96 hr (n = 20 from distress call group) following hatching. Previous studies

have revealed that unmanipulated chicks show a naive auditory preference for the bobwhite maternal call over species-atypical maternal calls at both 24 and 48 hr following hatching, but require combined maternal auditory and maternal visual cues to direct social preferences by 72 hrs following hatching. Once chicks reach the developmental stage where they utilize visual cues to direct preferential behavior, this effect is persistent (Lickliter, 1994; Lickliter & Virkar, 1989). During the simultaneous-choice tests, subjects were presented with identical species-typical auditory cues (the bobwhite maternal call) paired with a stuffed model of a bobwhite hen or a stuffed model of a species-atypical scaled quail hen. In other words, during testing both hen models were emitting the same species-typical bobwhite call, requiring subjects to direct their social preference on the basis of available static visual cues (as the identical available auditory cues did not allow a basis for decision). Choice, latency, and duration measures were scored as described in General Methods.

Results and Discussion

The results of testing are shown in Tables 5 and 6. Chicks exposed to 10 min/hr of bobwhite distress calls did not exhibit a preference for either hen model at any age

tested. Chi-square values were as follows: 24 hrs = 3.71, 72 hrs = .42, and 96 hrs = 3 (degrees of freedom = 2 in all cases). Correspondingly, there were no significant differences in the subjects' latency and duration scores for either of the stimuli presented during testing at any age.

These findings stand in contrast to results obtained from unmanipulated chicks in previous experiments (Lickliter, 1994; Lickliter & Virkar, 1989). In these studies, unmanipulated chicks did not demonstrate a preference for the species-typical visual cues over the species-atypical visual cues at 24 and 48 hr following hatching, but did show a preference for combined maternal auditory and maternal visual cues by 72 hr following hatching (see Table 2). In the present experiment, chicks exposed to 10 min/hr of bobwhite chick distress calls failed to demonstrate a preference for the bobwhite maternal auditory/visual cues at any age tested, indicating interference with species-typical patterns of intersensory development.

In contrast, chicks exposed to 10 min/hr of bobwhite contentment calls showed a significant preference for the stuffed bobwhite hen over the species-atypical stuffed scaled quail hen by 48 hr following hatching, indicating an

acceleration in species-typical visual responsiveness ($p < .01$). Chi-square values were as follows: 24 hrs = 2.33, 48 hrs = 11.41, and 72 hrs = 12.51 (degrees of freedom = 2 in all cases). Analysis of duration scores revealed that chicks showed significantly longer duration in their response to the stuffed bobwhite hen than to the stuffed scaled quail hen by 48 hr of age and showed significantly shorter latencies to the stuffed bobwhite hen by 72 hr of age ($p < .05$ in all cases).

These findings are similar to results obtained from a previous study in which embryos were similarly exposed prenatally to 10 min/hr of bobwhite chick contentment calls (Lickliter & Stoumbos, 1991). Chicks in that experiment demonstrated a significant preference for the stuffed bobwhite hen over the stuffed scaled quail hen by 24 hr of age. In the present experiment, chicks exposed to 10 min/hr of bobwhite chick contentment calls did not exhibit this preference for the bobwhite hen until 48 hr of age. Although the results are not identical, both indicate acceleration in species-typical patterns of visual responsiveness.

Taken together, the findings from the present study

suggest that the type of stimulation encountered prenatally mediates the course of perceptual development.

Specifically, 10 min/hr of bobwhite distress calls appears to interfere with species-typical perceptual development, whereas 10 min/hr of bobwhite contentment calls appears to accelerate species-typical visual responsiveness.

In sum, Experiments 1A and 1B explored how two distinct types of auditory stimulation presented prenatally can impact perceptual organization when the amount of stimulation is held constant across conditions. The question arises as to what effect a lesser amount of either distress or contentment vocalizations might have on perceptual development. For example, would 5 min/hr of prenatal exposure to bobwhite contentment calls have the same impact on postnatal auditory responsiveness as 10 min/hr of exposure to the same stimulus? Similarly, would a reduction in amount of stimulation differ depending on the type of auditory stimulation encountered? The purpose of the next two experiments was to further unpack this relationship between type of stimulation and amount of stimulation during the prenatal period.

Experiment 2A: Effects of 5 Min/Hr of Prenatal Exposure to Bobwhite Contentment Calls or Bobwhite Distress Calls on Postnatal Auditory Responsiveness

Method

120 bobwhite quail embryos, drawn from fourteen separate hatches, served as subjects. The shell and membrane over the air space of the egg of each subject were removed as described in the General Methods section. After this procedure, subjects were incubated in groups of 10 to 12 same-aged embryos. Subjects were stimulated for 5 min per hour for a minimum of 24 hr from the second half of Day 21 to the second half of Day 22 of incubation. Sixty embryos were exposed to recorded bobwhite hatchling contentment vocalizations. A second group of sixty embryos was exposed to bobwhite hatchling distress vocalizations. All subjects were given a simultaneous-choice test between a bobwhite maternal call and a chicken maternal call at either 24 hr (n = 20 from contentment call group and n = 20 from distress call group), 72 hr (n = 20 from contentment call group and n = 20 from distress call group) or 96 hr (n = 20 from contentment call group and n = 20 from distress call group) following hatching. Choice, latency and duration measures were scored as described in General Methods.

Results and Discussion

Testing results are shown in Tables 7 and 8. Chicks exposed prenatally to 5 min/hr of bobwhite chick distress calls and chicks exposed to 5 min/hr of bobwhite chick contentment calls both demonstrated a significant preference for the species-specific bobwhite maternal call over a chicken maternal call at all ages tested ($p < .01$ in all cases). Chi-square values following exposure to bobwhite distress calls were as follows: 24 hrs = 36, 72 hrs = 18.1, and 96 hrs = 32. Chi-square values following exposure to bobwhite contentment calls were as follows: 24 hrs = 36, 72 hrs = 36, and 96 hrs = 19.2 (degrees of freedom = 2 in all cases). Analysis of latency and duration scores supported these results, with chicks showing significantly shorter latencies and longer durations in their response to the bobwhite maternal call than to the species-atypical chicken maternal call ($p < .01$ in all cases). These findings suggest that 5 min/hr of prenatal exposure to either bobwhite distress calls or bobwhite contentment calls results in altered patterns of postnatal species-typical perceptual responsiveness.

Interestingly, the results from embryos exposed to only 5 min/hr of both types of prenatal auditory stimulation parallel the results from embryos exposed to 10

min/hr of the same type of prenatal auditory stimulation (Experiment 1A), indicating that exposing embryos to enhanced auditory stimulation appears to facilitate their continued responsiveness to maternal auditory cues into later stages of postnatal development.

The purpose of the next experiment was to assess whether the effects of 5 min/hr prenatal exposure to bobwhite contentment calls generalizes to responsiveness in other sensory systems by examining the effect of this exposure on chicks' postnatal visual, rather than auditory, responsiveness to maternal cues.

Experiment 2B: Effects of 5 Min/Hr of Prenatal Exposure to Bobwhite Contentment Calls or Bobwhite Distress Calls on Postnatal Auditory/Visual Responsiveness

Method

120 bobwhite quail embryos, drawn from fourteen separate hatches, underwent the same procedure as subjects in the previous experiment. Subjects were tested at either 24 hr (n = 20 from contentment call group and n = 20 from distress call group), 48 hr (n = 20 from contentment call group), 72 hr (n = 20 from contentment call group and n = 20 from distress call group) or 96 hr (n = 20 from distress call group) following hatching. During the simultaneous-choice tests, subjects were presented with identical

species-typical auditory cues (the bobwhite maternal call) paired with a stuffed model of a bobwhite hen or a stuffed model of a species-atypical scaled quail hen, as in Experiment 1B. Choice, latency, and duration measures were scored as described in General Methods.

Results and Discussion

The results of testing are shown in Tables 9 and 10. Chicks exposed prenatally to 5 min/hr of bobwhite chick distress calls did not show a preference for either hen model at any age tested. Chi-square values were as follows: 24 hrs = 4.91, 72 hrs = .12, and 96 hrs = 0 (degrees of freedom = 2 in all cases). Correspondingly, there were no significant differences in the subjects' latency and duration scores for either of the stimuli presented at any age tested. These findings suggest that 5 min/hr of prenatal exposure to bobwhite chick distress calls serves to interfere with species-typical patterns of perceptual development.

In contrast, chicks exposed prenatally to 5 min/hr of bobwhite chick contentment calls demonstrated a significant preference for the species-specific bobwhite hen over the scaled quail hen by 72 hr following hatching ($p < .01$). Chi-square values were as follows: 24 hrs = .74, 48 hrs = 2.24, and 72 hrs = 13 (degrees of freedom = 2 in all

cases). Analysis of latency and duration scores supported these results, with chicks showing significantly shorter latencies and longer durations in their response to the bobwhite hen than to the scaled quail hen by 72 hr of age ($p < .05$ in all cases). These findings parallel the pattern of visual responsiveness seen in unmanipulated chicks in previous studies in this series (Lickliter, 1994; Lickliter & Virkar, 1989), suggesting that 5 min/hr of bobwhite contentment calls does not appear to alter species-typical visual responsiveness.

Experiment 3: Observations of Unmanipulated Embryos, Embryos Exposed to Bobwhite Distress Calls, and Embryos Exposed to Bobwhite Contentment Calls

An important step in understanding the effects of different types of auditory stimulation on early prenatal perceptual organization is to explore the possible underlying mechanisms involved. As previously suggested, one explanation for changes in perceptual responsiveness as a result of manipulations of sensory stimulation is resulting changes in the young organism's overall arousal level. This arousal-based mechanism is presumed to be regulated by some optimal level of overall sensory stimulation, which makes it possible for the embryo to attend and respond to sensory experience present in the

prenatal environment (see Lickliter & Lewkowicz, 1995; Radell & Gottlieb, 1992).

Vocalizations appear to be indicative of behavioral arousal level in precocial avian species, with low arousal associated with none to infrequent vocalizations and high arousal associated with a rapid rate of vocalizations (Gottlieb, 1971, 1993; Gray, 1990). According to Gray (1990), a heightened state of arousal, as indicated by frequent vocalizations, should decrease sensitivity to environmental conditions. For example, McBride and Lickliter (1993) found that partially isolated bobwhite chicks (i.e., chicks that had the opportunity to see one sibling through a glass divider but not physically contact that sibling) frequently emitted distress calls during the first 72 hr following hatching and did not exhibit species-typical responsiveness to auditory/visual maternal cues. It is possible that a high state of arousal may have interfered with the chicks' attentiveness to visual experience with conspecifics, which has been found to be necessary for the development of visually based maternal recognition (McBride & Lickliter, 1993; see Gottlieb, 1993 for a similar auditory example with ducklings).

In a similar vein, Gottlieb (1971) found that bill claps were a reliable behavioral index of prenatal auditory

discrimination in mallard ducklings. Specifically, the rate of bill-clapping increased when embryos were exposed to their species-typical maternal call, but not for species-atypical maternal calls or for sibling calls. Further research revealed that bill-clapping may be indicative of an increase in overall behavioral response to particular stimulation, rather than limited solely to bill movements. For example, head and body movement also provide a useful probe of auditory discrimination ability in ducklings (Gottlieb, 1971).

The present experiment used prenatal vocalizations, bill claps and body and head movements as behavioral measures to assess the presence of behavioral states that may be associated with particular stimulation and may contribute to subjects' behavior during subsequent postnatal testing trials.

Method

Forty-eight bobwhite embryos, drawn from five separate hatches, served as subjects. To facilitate access to the embryos and delivery of modified sensory stimulation, the shell and inner-shell membrane over the air space of the egg of each subject were removed and the embryos' head was gently pulled out of the shell during the second half of the 21st day of incubation. Following this procedure, the

opened eggs were placed in a portable incubator, which is outfitted with a clear Plexiglas top, allowing audio and visual recording of the activities of the embryos within. Recording was done with a Panasonic Model AG-185 tripod mounted VHS video camera. After a 4 hr acclimation period, observations of individual embryos began. Each embryo's behavior was recorded on video tape for three 20 min periods, one at 4 hr following egg opening, one at 12 hr following egg opening and one at 20 hr following egg opening. Each 20 min period was divided into four 5 min session. Two of these sessions were stimulation periods (S) and two were nonstimulation periods (NS), which allowed each embryo to serve as its own control. Half of the embryos received these sessions in the order S-NS-S-NS, while the other half received the order NS-S-NS-S. In this way, any short term effects (within 5 min) of stimulation should have been detected. Embryos were exposed to either bobwhite hatchling distress calls (n = 16) or bobwhite hatchling contentment calls (n = 16) during the stimulation periods. A control group (n = 16) received no modified sensory stimulation and were monitored for the equivalent 20 min of observation. Independent raters blind to the experimental design coded the resulting audio and visual tapes for activity and vocalization levels. A minimum of

two raters was used in each experimental group, affording measures of interobserver reliability ($\underline{r} = .93$ for behavioral activity measure and $\underline{r} = .98$ for vocalization measure).

Ratings of the embryos' behavioral activity (bill claps, head and body movements) were made during each 5 min period, and activity during stimulation sessions were compared to the nonstimulation periods. If a period of quiescence (no observable movements) lasting 5 sec or longer occurred, this was scored as an inactivity phase. If bill claps or head movements or body movements were observed or if shorter periods of quiescence occurred (4 sec or less), an activity phase was scored. The total amount of 5 sec activity phases were totaled in both stimulation and nonstimulation period. Recordings of the embryos' vocalizations were also counted during each 5 minute period (see Appendix B for a sample rating sheet).

To evaluate the statistical reliability of changes in behavioral activity during the stimulation period, the Wilcoxon matched-paired signed-ranks test was employed. This nonparametric test compared each embryo's performance in the stimulation periods with its performance in the nonstimulation periods, specifically taking into account the direction of change and magnitude of change in

activity. If the direction of change in movements was consistent for all the embryos in a group, then the magnitude of change can be small and still achieve statistical reliability. If only a majority of embryos shared a certain direction of change, the magnitude of the majority's change had to be large and the magnitude of change in the minority's performance had to be relatively small. Since individual variation in baseline rates was likely, the Wilcoxon test seemed particularly appropriate in the present context. If different types of prenatal sensory stimulation result in different behavioral arousal levels in embryos, then significant differences between the control group and the exposure groups and between the two exposure groups should be observed.

Due to the smaller sample size ($n = 4$) in recording vocalizations, dependent t-tests were employed to analyze vocalization rates. The smaller sample size resulted from the inability to distinguish which individual bird emitted the recorded vocalization. Thus, the vocalizations emitted under each condition were recorded in four groups, with each group consisting of four embryos.

Results and Discussion

Results of the behavioral activity measure are shown in Table 11. Results of the vocalization measure are shown

in Table 12. First, a Mann Whitney test was employed to compare the number of activity phases in the initial non-stimulation period for the group that received the NS-S-NS-S regime with the group that received the S-NS-S-NS regime. This procedure was completed for both the chicks exposed to contentment calls and for the chicks exposed to distress calls. No statistically significant differences were found, suggesting that the effects seen during the assessment period were not due to immediate carry over effects from exposure to stimulation.

Similarly, a dependent t-test revealed that there were no differences in number of vocalizations in the initial stimulation and the initial non-stimulation period as a result of order of presentation.

Because there were no differences between birds who received a non-stimulation period first and birds who received a non-stimulation period following a stimulation period, the number of activity phases in both of the 5 min non-stimulation segments were combined and the number of activity phases in both of the 5 min stimulation segments were combined. In this way, each bird had a total number of activity phases for 10 min worth of stimulation and 10 min worth of non-stimulation. Wilcoxon Signed-Ranks tests were employed for each experimental condition (exposure to

contentment call or distress calls) to compare behavioral activity during stimulation periods with activity during non-stimulation periods. No statistically significant differences were found between the number of activity phases during non-stimulation and the number of activity phases during stimulation in each experimental condition. Dependent t-tests also revealed no statistically significant differences between the number of vocalizations during non-stimulation and the number of vocalizations during stimulation in each experimental condition.

Because there were no within-group differences between cells in either of the experimental groups, the number of activity phases for each of the two stimulation and two non-stimulation periods were collapsed into a total number of activity phases for each bird. A 3 (time of assessment) X 3 (type of call) factorial design was employed. The time of assessment (4, 12, or 20 hr following egg opening) constituted a within-subjects factor, while the type of call (distress, contentment, or control) constituted a between-subjects factor. This analysis revealed no significant interaction. However, a main effect for time of assessment was found, $F(2,90) = 12.13$, $p < .01$. A Scheffe post-hoc test revealed that the number of movements at 4 hr was significantly less than number of movements at

20 hr for each of the groups. A main effect was also demonstrated for type of exposure, $F(2,45) = 15.79$, $p < .01$. A Scheffe post-hoc test revealed that birds exposed to either distress calls or to contentment calls had significantly more activity phases than did birds in the control group. It is important to note that although birds in both experimental conditions exhibited more behavior than control birds, the two experimental conditions were not significantly different from one another.

These findings suggest that there may be behavioral states associated with particular sensory stimulation regimes. Specifically, augmented auditory stimulation (whether contentment or distress vocalizations) appeared to foster an increase in physical responsiveness when compared to controls. These states may mediate the differential patterns of responsiveness seen in birds from either of the two experimental conditions and birds from the control condition.

The increase in movement seen across time may reflect the onset and continuation of movements associated with hatching. Recall that bobwhite quail chicks typically hatch during the 23rd day of incubation. On Day 21, the embryo's bill usually penetrates the air space at the large end of the egg and, at this time, the embryo begins

to respire and vocalize (Freeman & Vince, 1974). This penetration of the air space also signals the beginning of the hatching process, which typically lasts from 24 to 36 hrs (Oppenheim, 1968).

For the vocalization measure, a 3 (time of assessment) X 3 (type of call) factorial design was also employed. This analysis revealed no main affect for time of assessment, $F(2,27) = 1.71$, no main effect for type of call, $F(2,27) = 1.8$, and no significant interaction, $F(4,27) = 1.8$. Thus, the assessment of behavioral activity appears to be a more sensitive probe than assessment of vocalizations in determining possible organismic characteristics and states associated with particular stimulation regimes.

General Discussion

As illustrated in Fig. 1, the results of this study demonstrate that augmented amounts of prenatal auditory stimulation can result in interference or acceleration of species-typical patterns of early perceptual development, depending on the particular type of auditory stimulation to which the embryo is exposed. In particular, results indicate that exposure to either 10 min/hr or 5 min/hr of bobwhite chick distress calls interferes with species-

typical patterns of postnatal intersensory responsiveness. Specifically, chicks in both of these conditions displayed a continued reliance on maternal auditory cues into late stages of postnatal development (Experiment 1A and 2A) and failed to respond to maternal visual cues at ages when normally reared chicks exhibit this species-specific ability (Experiment 1B and 2B). In contrast, prenatal exposure to 10 min/hr of bobwhite contentment calls resulted in a continued preference for maternal auditory cues into late stages of development (Experiment 1A) and an acceleration in preferential responsiveness to maternal visual cues (Experiment 1B). Chick exposed to only 5 min/hr of bobwhite contentment calls demonstrated a continued preference for maternal auditory cues into late stages of postnatal development (Experiment 2A) and exhibited species-typical responsiveness to maternal visual cues (Experiment 2B). In sum the findings from the present study indicate that exposure to augmented amounts of prenatal auditory stimulation does not, in and of itself, interfere with postnatal perceptual functioning. Rather, the amount of auditory stimulation and the type of auditory stimulation appear to interact to determine subsequent

perceptual functioning. In fact, the type of auditory stimulation appears to be a more important factor than the amount of stimulation presented.

Interestingly, in all conditions in the present study chicks exposed to enhanced prenatal auditory stimulation continued to respond to maternal auditory cues beyond the age when unmanipulated chicks no longer respond to auditory cues. These results are consistent with a previous experiment which demonstrate that bobwhite quail chicks exposed to particular sensory stimulation during the prenatal period prefer postnatal testing stimuli that match their prior experience (McBride & Lickliter, 1995). In addition, chicks in that experiment displayed a postnatal preference for familiar types of sensory stimuli over familiar amounts of sensory stimuli (McBride & Lickliter, 1995). Taken together, these results indicate the existence of a hierarchical relationship between these two features of sensory stimulation. Specifically, the type of stimulation appears to be a more influential feature of sensory stimulation than is amount of stimulation.

Results from previous experiments with bobwhite chicks support this notion that the type of stimulation

encountered is a crucial factor in perceptual development. For example, Sleigh, Columbus, and Lickliter (in press) demonstrated that embryos exposed to bobwhite contentment calls during the early prenatal period exhibited auditory learning, whether they were incubated socially or in isolation. In contrast, embryos exposed to bobwhite distress calls failed to demonstrate auditory learning, whether they were incubated socially or in isolation. Similarly, Lickliter and Stoumbos (1991) demonstrated that increased amounts of bobwhite contentment calls accelerate postnatal responsiveness to maternal cues, while increased amounts of bobwhite contentment calls with a faster than normal repetition rate do not result in this acceleration. In a similar vein, McBride and Lickliter (1994) found that chicks exposed to bobwhite distress calls during early postnatal development exhibit species-atypical patterns of perceptual development. In contrast, chicks exposed to bobwhite contentment calls during early postnatal development exhibit species-typical patterns of perceptual development.

Although the type of stimulation available to the developing embryo or neonate has emerged as an important

variable in perceptual development, the amount of sensory stimulation should not be overlooked as an important factor in species-typical perceptual development. As suggested by Radell and Gottlieb (1992), sensory stimulation that falls within some optimal range appears to maintain or facilitate normal patterns of perceptual functioning (Lickliter, 1990; Lickliter & Stoumbos, 1991; Radell & Gottlieb, 1992). On the other hand, substantially attenuated or substantially increased amounts of stimulation appear to interfere with both the emergence of species-typical patterns of intersensory functioning (Gottlieb, 1993; Lickliter & Lewkowicz, 1995; Sleigh & Lickliter, 1995) and prenatal auditory learning (Gottlieb et al, 1989; Lickliter & Hellewell, 1992; Lickliter & Lewkowicz, 1995; Radell & Gottlieb, 1992; Sleigh & Lickliter, 1995). In light of the present experiment, the amount of stimulation that is considered within the optimal range may be dependent upon the particular type of sensory stimulation that is being encountered. For example, both 5 min/hr and 10 min/hr of bobwhite distress calls appear to fall outside the range considered optimal, whereas both 5 min/hr and 10 min/hr of bobwhite contentment calls appear to fall within the range

considered optimal. Future studies should examine the impact of prenatal exposure to substantially increased amounts of bobwhite contentment calls on subsequent postnatal perceptual development to determine if greatly augmented amounts of this type of stimulation can result in altered species-typical visual responsiveness.

Future studies should also address the specific features of sensory stimulation that mediate patterns of perceptual responsiveness. For example, previous work has demonstrated that precocial avian embryos are sensitive to repetition rates (notes per second) of auditory stimulation (Gottlieb, 1981; Miller, 1983). For example, Miller (1983) manipulated the repetition rates of a mallard duckling call and demonstrated that slow repetition rates were associated with behavioral inhibition in mallard ducklings, whereas faster repetition rates were associated with behavioral excitation. These findings suggest that repetition rates may mediate arousal levels in the young organism and impact subsequent perceptual responsiveness. In this light, Sleigh, Columbus, and Lickliter (in press) exposed isolation incubated embryos to 10 min/hr of bobwhite contentment calls with a faster than normal repetition rate

(similar to the repetition rate of bobwhite distress calls). Isolate incubated embryos exposed to the accelerated contentment calls demonstrated auditory learning. In the same study, isolate incubated embryos exposed to unmanipulated contentment calls exhibited auditory learning, whereas isolate incubated embryos exposed to unmanipulated distress calls failed to show auditory learning. In other words, isolate incubated embryos exposed to either normal or accelerated contentment calls displayed similar outcomes, suggesting that repetition rate, in and of itself, did not affect the observed patterns of responsiveness. In this light, Heaton, Miller, and Goodwin 1978) suggested that frequency modulation and/or fundamental frequency are likely important acoustic features that direct bobwhite chicks' species-specific auditory preferences. Future studies should address this possibility.

While the present study utilized behavioral activity and vocalizations as measures to assess the presence of behavioral states associated with particular stimulation regimes, what remains to be fully explored are other organismic aspects of the relationship between amount and

type of stimulation experienced and subsequent perceptual behavior patterns. Specifically, the arousal level and attentional capacities of the organism in its developmental context should be more thoroughly examined. As previously discussed, the number of vocalizations emitted by embryos did not differ significantly regardless of which stimulation regime the embryos experienced. In contrast, measures of behavioral activity did differentiate the two experimental conditions from the control condition, but did not differentiate the two experimental conditions from each other. Thus, a more sensitive measure may be needed to understand the role of behavioral states associated with particular stimulation regimes in mediating perceptual development. For example, future studies could examine whether specific types of prenatal sensory stimulation result in differential physiological responsiveness. Measures of heart rate and respiration rate of precocial avian embryos has been successfully utilized in a number of studies of embryonic sensitivity to sensory stimulation (e.g., Gottlieb, 1971; Ockleford & Vince, 1977; Vince, Ockleford, & Reader, 1984). In a similar vein, Smotherman and Robinson (1992) found persistent and reliable

physiological effects in rat fetuses provided brief exposure to milk prenatally.

Under normally occurring conditions, limits in the amount and type of sensory stimulation experienced is provided by the structured developmental system of the egg, allowing an orderly structure for the developing embryo that is essentially similar across members of a species. This notion of an orderly context for development is consistent with a view of development that recognizes the organism-environment relationship is one that is structured on both sides. The epigenetic emergence of early perceptual organization is both directed and constrained by features of the organism as well as those of its developmental context. In this way, perceptual organization is actively constructed during the course of each individual's development.

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Table 1. Preference of Control Chicks in Simultaneous Auditory Choice Tests (Lickliter & Virkar, 1989).

Age (in hrs)	n	n responding	Preference		
			Bobwhite Maternal Call	Chicken Maternal Call	No Preference
24	21	21	17*	0	4
48	22	22	14*	1	7
72	23	23	7	5	11
96	21	21	0	0	21

* $p < .001$ (binomial test)

Table 2. Preference of Control Chicks in Simultaneous Auditory-Visual Choice Tests (Lickliter & Virkar, 1989).

Age (in hrs)	n	n responding	Preference		
			Bobwhite Hen with Bobwhite Maternal Call	Scaled Hen with Bobwhite Maternal Call	No Preference
72	22	22	19*	1	2
96	20	20	17*	0	3

* $p < .001$ (binomial test)

Table 3. Preference of Chicks in Simultaneous Auditory Choice Tests in Experiment 1A.

Age (in hrs)	n	n responding	Preference		
			Bobwhite Maternal Call	Chicken Maternal Call	No Preference
10 MIN/HR BOBWHITE DISTRESS CALLS					
24	20	20	20*	0	0
72	20	14	14*	0	0
96	20	13	13*	0	0
10 MIN/HR BOBWHITE CONTENTMENT CALLS					
24	20	19	19*	0	0
72	20	17	14*	1	2
96	20	13	11*	1	1

* $p < .01$ (chi-square test)

Table 4. Means and Standard Deviations of Latency and Duration Scores of Chicks in Simultaneous Auditory Choice Tests in Experiment 1A.

Age (in hrs)	n	Latency		Duration	
		Bobwhite Maternal Call	Chicken Maternal Call	Bobwhite Maternal Call	Chicken Maternal Call
10 MIN/HR BOBWHITE DISTRESS CALLS					
24	20	31.8* (22.3)	300 (0)	125.25* (62.66)	0 (0)
72	14	66.5* (55.65)	300 (0)	122.1* (128.11)	0 (0)
96	13	118.05* (137.46)	281.1 (58.25)	59.75* (59.03)	2.0 (6.16)
10 MIN/HR BOBWHITE CONTENTMENT CALLS					
24	19	43.45* (66.35)	300 (0)	154.45* (58.78)	0 (0)
72	17	85.9* (112.07)	230.5 (111.85)	71.55* (63.93)	4.0 (7.25)
96	13	163.1* (124.29)	266.45 (85.72)	50.05* (58.59)	3.2 (9.04)

* $p < .01$ (Wilcoxon signed-ranks)

Table 5. Preference of Chicks in Simultaneous Auditory-Visual Choice Tests in Experiment 1B.

Age (in hrs)	n	n responding	Preference		
			Bobwhite Hen with Bobwhite Maternal Call	Scaled Hen with Bobwhite Maternal Call	No Preference
10 MIN/HR BOBWHITE DISTRESS CALLS					
24	20	20	10	7	3
72	20	19	5	7	7
96	20	18	9	6	3
10 MIN/HR BOBWHITE CONTENTMENT CALLS					
24	20	18	5	9	4
48	20	17	12*	1	4
72	20	16	12*	2	2

* $p < .01$ (chi-square test)

Table 6. Means and Standard Deviations of Latency and Duration Scores of Chicks in Simultaneous Auditory-Visual Choice Tests in Experiment 1B.

Age (in hrs)	n	Latency		Duration	
		Bobwhite Hen with Bobwhite Maternal Call	Scaled Hen with Bobwhite Maternal Call	Bobwhite Hen with Bobwhite Maternal Call	Scaled Hen with Bobwhite Maternal Call
10 MIN/HR BOBWHITE DISTRESS CALLS					
24	20	112.95 (113.06)	136.95 (126.97)	94.25 (82.95)	67.3 (75.03)
72	19	121.95 (118.55)	103.1 (108.91)	50.6 (41.99)	66.2 (62.3)
96	18	126.65 (120.54)	154.3 (116.01)	43.8 (44.37)	32.6 (41.76)
10 MIN/HR BOBWHITE CONTENTMENT CALLS					
24	18	173.15 (131.65)	122.2 (119.04)	58.55 (80.65)	84.75 (82.0)
48	17	116.6 (105.24)	184.2 (123.38)	63.45* (50.73)	23.95 (35.56)
72	16	126.6* (115.92)	192.7 (121.67)	63.6* (54.97)	19.9 (31.75)

* $p < .05$ (Wilcoxon signed-ranks)

Table 7. Preference of Chicks in Simultaneous Auditory Choice Tests in Experiment 2A.

Age (in hrs)	n	n responding	Preference		
			Bobwhite Maternal Call	Chicken Maternal Call	No Preference
5 MIN/HR BOBWHITE DISTRESS CALLS					
24	20	17	17*	0	0
72	20	19	15*	1	3
96	20	16	16*	0	0
5 MIN/HR BOBWHITE CONTENTMENT CALLS					
24	20	18	18*	0	0
72	20	18	18*	0	0
96	20	15	13*	1	1

* $p < .01$ (chi-square test)

Table 8. Means and Standard Deviations of Latency and Duration Scores of Chicks in Simultaneous Auditory Choice Tests in Experiment 2A.

Age (in hrs)	n	Latency		Duration	
		Bobwhite Maternal Call	Chicken Maternal Call	Bobwhite Maternal Call	Chicken Maternal Call
5 MIN/HR BOBWHITE DISTRESS CALLS					
24	17	72.9* (107.51)	274.65 (78.03)	123.35* (83.0)	1.5 (4.62)
72	19	66.7* (93.58)	242.35 (98.65)	93.25* (67.61)	8.35 (19.95)
96	16	111.75* (111.77)	300 (0)	57.6* (35.57)	0 (0)
5 MIN/HR BOBWHITE CONTENTMENT CALLS					
24	18	59.55* (84.74)	300 (0)	129.1* (62.38)	0 (0)
72	18	62.7* (88.41)	300 (0)	88.55* (56.91)	0 (0)
96	15	131.25* (131.15)	266.05 (82.96)	47.5* (48.38)	3.25 (8.97)

* $p < .01$ (Wilcoxon signed-ranks)

Table 9. Preference of Chicks in Simultaneous Auditory-Visual Choice Tests in Experiment 2B.

Age (in hrs)	n	n responding	Preference		
			Bobwhite Hen with Bobwhite Maternal Call	Scaled Hen with Bobwhite Maternal Call	No Preference
5 MIN/HR BOBWHITE DISTRESS CALLS					
24	20	20	6	11	3
72	20	16	6	5	5
96	20	18	6	6	6
5 MIN/HR BOBWHITE CONTENTMENT CALLS					
24	20	19	6	8	5
48	20	17	6	8	3
72	20	14	11*	2	1

* $p < .01$ (chi-square test)

Table 10. Means and Standard Deviations of Latency and Duration Scores of Chicks in Simultaneous Auditory-Visual Choice Tests in Experiment 2B.

Age (in hrs)	n	Latency		Duration	
		Bobwhite Hen with Bobwhite Maternal Call	Scaled Hen with Bobwhite Maternal Call	Bobwhite Hen with Bobwhite Maternal Call	Scaled Hen with Bobwhite Maternal Call
5 MIN/HR BOBWHITE DISTRESS CALLS					
24	20	71.9 (89.74)	82.25 (97.56)	83.65 (80.77)	105.75 (67.96)
72	16	149.25 (127.35)	115.5 (126.44)	76.55 (75.44)	80.55 (82.22)
96	18	159.3 (111.29)	151.45 (117.4)	39.3 (50.62)	59.6 (68.74)
5 MIN/HR BOBWHITE CONTENTMENT CALLS					
24	19	85.75 (99.06)	82.35 (100.87)	69.35 (59.87)	83.85 (67.86)
48	17	154.55 (128.5)	126.65 (113.85)	42.7 (50.91)	62.2 (74.65)
72	14	134.45* (120.88)	219.4 (127.08)	56.35* (56.67)	17.35 (34.78)

* $p < .05$ (Wilcoxon signed-ranks)

Table 11. Means and Standard Deviations of Number of Behavioral Activity Periods of Chicks in Experiment 3.

	Distress Call	Contentment Call	Control
4 hrs	88.56 (30.81)	100.38 (37.37)	53.81 (27.72)
12 hrs	115.88 (33.59)	123.81 (30.53)	71.69 (31.77)
20 hrs	113.19 (27.67)	122.56 (32.45)	99.50 (41.08)

* $p < .05$ (3 x 3 ANOVA)

Table 12. Means and Standard Deviations of Number of Vocalizations of Chicks in Experiment 3.

	Distress Call	Contentment Call	Control
4 hrs	5 (5.87)	12.75 (13.29)	22.5 (9.96)
12 hrs	17.5 (14.92)	3 (1.22)	22.5 (15.53)
20 hrs	18.25 (20.13)	26 (30.06)	35 (20.06)

	Hours Posthatching			
	24	48	72	96
Normal, Unstimulated Controls (Lickliter & Virkar, 1989; Lickliter, 1990b)	□ ●	□ ●	■ ○	
10 min/hr Distress Calls (Experiments 1A & 1B)	□ ●		□ ●	□ ●
5 min/hr Distress Calls (Experiments 2A & 2B)	□ ●		□ ●	□ ●
10 min/hr Contentment Calls (Experiments 1A & 1B)	□ ●	○	□ ○	□
10 min/hr Contentment Calls (Stoumbos & Lickliter, 1991)	□ ○			
5 min/hr Contentment Calls (Experiments 2A & 2B)	□ ●	●	□ ○	□

□ Preference for Species Specific Auditory Cues	○ Preference for Species Specific Visual Cues
■ No Preference for Species Specific Auditory Cues	● No Preference for Species Specific Visual Cues

Figure 1. Summary of the postnatal preferences of bobwhite chicks for maternal auditory and visual cues following normal or augmented prenatal auditory experience.

Appendix A

SAMPLE SCORING SHEET FOR SIMULTANEOUS-CHOICE TESTS

GROUP: _____ WEEK: _____ SUBJECT: _____

DAY 23: _____ HATCHED: _____ TESTER: _____

TEST 1

DATE: _____ TIME: _____ AGE: _____

STIMULUS A: LATENCY: _____ DURATION: _____

STIMULUS B: LATENCY: _____ DURATION: _____

COMMENTS:

TEST 2

DATE: _____ TIME: _____ AGE: _____

STIMULUS A: LATENCY: _____ DURATION: _____

STIMULUS B: LATENCY: _____ DURATION: _____

COMMENTS:

Appendix B

SAMPLE VOCALIZATION RECORDING SHEET

OBSERVER: _____

CONDITION OBSERVED: _____

Date of Observation: _____

Week 1: 5min (stim) 5 min(non-stim) 5 min (stim) 5 min(non-stim)

**4 hrs following
egg opening**

**12 hrs following
egg opening**

**20 hrs following
egg opening**

Date of Observation: _____

Week 2: 5min (non-stim) 5 min(stim) 5 min (non-stim) 5 min(stim)

**4 hrs following
egg opening**

**12 hrs following
egg opening**

**20 hrs following
egg opening**

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1989 - 1992

PUBLICATIONS IN REFEREED JOURNALS:

Sleigh, M. J. & Lickliter, R. (in preparation) Timing of Prenatal Auditory Experience Alters Postnatal Responsiveness in Bobwhite Quail.

Sleigh, M. J., Columbus, R. F., & Lickliter, R. (in preparation). Postnatal experience with maternal cues alters species-typical perceptual responsiveness in bobwhite quail.

Sleigh, M. J., Columbus, R. F., & Lickliter, R. (in press). Type of prenatal sensory experience affects prenatal auditory learning in bobwhite quail chicks. Journal of Comparative Psychology.

Sleigh, M. J., & Lickliter, R. (in press). Type and amount of prenatal stimulation alters perceptual responsiveness in bobwhite quail chicks. Infant Behavior and Development.

Sleigh, M. J., & Lickliter, R. (1995). Augmented prenatal visual stimulation alters postnatal auditory and visual responsiveness in bobwhite quail chicks. Developmental Psychobiology, 28, 353-366.

EDITED BOOKS:

Sleigh, M. J., Columbus, R. F., & Sgro, J. A. (1996). Exploring Introductory Psychology. New York: McGraw-Hill Publishing Company.

PAPERS PRESENTED AT SCIENTIFIC MEETINGS:

Sleigh, M. J., Columbus, R. F., & Lickliter, R. Amount and type of prenatal sensory stimulation affects prenatal auditory learning in bobwhite quail chicks. Accepted for presentation at the International Conference for Infant Studies, Providence, RI, April, 1996.

Columbus, R. F., Sleigh, M. J., & Lickliter, R. Postnatal experience with integrated or disparate maternal cues affects intersensory development in bobwhite quail. Accepted for presentation at the International Conference for Infant Studies, Providence, RI, April, 1996.

Sleigh, M. J., & Lickliter, R. Differential amounts of specific prenatal auditory stimulation alter postnatal responsiveness to maternal auditory and visual cues in bobwhite quail chicks. Presented at the International Society for Developmental Psychobiology Annual Meeting, San Diego, CA, November, 1995.

Columbus, R. F., Sleigh, M. J., & Lickliter, R. Postnatal experience with modified maternal auditory and visual cues alters intermodal responsiveness in bobwhite quail chicks. Presented at the International Society for Developmental Psychobiology Annual Meeting, San Diego, CA, November, 1995.

Sleigh, M. J., & Lickliter, R. Augmented prenatal visual stimulation alters postnatal perceptual functioning in bobwhite quail. Presented at the International Society for Developmental Psychobiology Annual Meeting, Islamorada, FL, November, 1994.

Zeskind, P. S., & Sleigh, M. J. Mothers' attitudes about infants are related to their perceptions of infant cries varying in pitch. Presented at the Biennial Conference on Human Development, Pittsburgh, PA, April, 1994.

GRANTS:

VPI & SU Graduate Research Development Grant (principal investigator), September, 1995

PROFESSIONAL SERVICE:

Graduate Student Honor Court Representative
VPI & SU, Blacksburg, VA
1993 - present

Psi Chi Treasurer
James Madison University, Harrisonburg, VA
1991 - 1992

PROFESSIONAL MEMBERSHIPS:

American Psychological Society, Student Member
International Society for Developmental Psychobiology, Student Member
International Society for Infant Studies, Student Member

HONORS AND AWARDS:

Sandra G. Weiner Developmental Psychobiology Student Investigator Award,
International Society for Development Psychobiology, November, 1994.

VPI & SU Graduate Student Travel Fund Award. August, 1995.

Second Place: VPI & SU Graduate Research Symposium. Augmented prenatal visual stimulation alters postnatal perceptual functioning in bobwhite quail. March, 1995

Psi Chi, National Psychology Honor Society
Sigma Tau Delta, National English Honor Society
Phi Kappa Phi, National Honor Society
Golden Key National Honor Society
National Dean's List

A handwritten signature in black ink, appearing to read 'M. Z. 182'.