THE EFFECTS OF AUGMENTED PRENATAL VISUAL STIMULATION ON POSTNATAL PERCEPTUAL RESPONSIVENESS IN BOBWHITE QUAIL

by

Merry J. Sleigh

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APPROVED:

R. Lickliter, Chair

R. P. Cooper

J. Germana

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(ABSTRACT)

The present study examined whether previously reported effects of altered prenatal sensory experience on subsequent acceleration of intersensory functions are mediated by mechanisms sensitive to the overall amount of stimulation. Results reveal that chicks exposed to augmented amounts of prenatal visual stimulation show interference in subsequent species-typical perceptual development. Specifically, chicks 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. Embryos in this study also failed to demonstrate early auditory learning of an individual maternal call, a behavior reliably seen in unmanipulated embryos. These findings suggest that substantially increased amounts of visual stimulation appear to prevent the emergence of species-typical patterns of intersensory functioning and lend support to the notion that stimulation that falls within some optimal range seems to maintain or facilitate normal patterns of perceptual functioning, while stimulation beyond the range of the species norm appears to result in intersensory interference.

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Introduction

The importance of the prenatal environment and its subsequent impact on postnatal perceptual organization has received increasing attention in recent years in the developmental literature (DeCasper & Spence, 1986; Gottlieb, 1988; Gottlieb, Tomlinson, & Radell, 1989; Lickliter 1990a,b; Radell & Gottlieb, 1992; Smotherman & Robinson, 1990; Turkewitz & Kenny, 1982, 1985). In the most general sense, this body of empirical and conceptual work demonstrates that the stimulation provided by prenatal conditions, whether typical or atypical, actively shapes the development of species-specific cognitive and perceptual capabilities. These prenatal conditions can interfere, maintain, or facilitate the various aspects of the organism's behavioral development (Gottlieb,1976).

One feature of early development that can play an active role in the construction of species-specific perceptual organization is the amount of stimulation that an organism experiences. T. C. Schnierla (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, Schnierla 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 indeed demonstrated that young organisms 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, and Smoller, 1988). 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 from other modalities.

According to Schnierla (1959, 1965), the organism's response to stimulation depends not only on the quantitative aspects of the stimulus, but also on the properties of the organism itself. The arousal level, the experiential history, and the developmental condition of an organism serve to mediate the influence of any given sensory stimulation. In a similar vein, Karmel, Gardner, and Magnano (1991) have suggested that, for the neonate, the world is simultaneously determined by both internal and external stimulation. In other words, arousal and attention are inextricably intertwined in early development and become distinct only as a product of experience. 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 altering the nature of sensory experience regardless of modality. In other words, the way an infant perceives a particular stimulus can be altered by changing the arousal level of the infant or by changing the characteristics of the stimulus.

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 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 exists must be explored, as well as the state and developmental history of the organism.

This pattern of reciprocal determination in the development of early perceptual responsiveness is only beginning to be understood. The specific mechanisms and experiences which lead to particular developmental outcomes in any sensory system afford a fertile testing ground for many of our conceptions regarding the process of epigenesis (Gottlieb, 1971, 1991). The culmination of recent empirical research in this area provides clues to unraveling the notion of effective intensity and how it translates into the emergence of early perceptual behavior.

For example, the perceptual development of birds can potentially provide insights into the intertwined relationship between attention and arousal. Similar to the human infant research, the response of bobwhite quail chicks to stimulation present in the environment differs depending on the amount of stimulation provided. Lickliter (1990a) 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 and a scaled 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 minutes/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 control chicks.

Taken together, the results from Lickliter (1990a) 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. In contrast to the wide spread assumption that simply increasing the amount of stimulation serves to facilitate early sensory development, Turkewitz and Kenny (1982; 1985) have suggested that limitation in early sensory experience provides an orderly structure for early sensory development. Sensory systems become functional at different times; therefore, each system can become operational without ongoing competition from other systems emerging simultaneously.

Unfortunately, Turkewitz and Kenny's (1985) theory does not account for all available findings, but it has proven of great heuristic value. 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 et al (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 minutes 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 if stimulation to immature sensory systems exceeds a certain level or threshold. Radell and Gottlieb (1992) suggest that sensory experience that falls within a range of stimulation typical for that species should not interfere with intersensory development. In fact, mildly enhanced levels of stimulation may maintain or <u>facilitate</u> typical development. This hypothesis would explain the previously discussed findings of Lickliter (1990a) 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.

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 argued a curvilinear relation between arousal and performance (Yerkes & Dodson, 1908). Excessive or reduced arousal levels are generally associated with poor performance, with a moderate level of arousal 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.

The arousal based mechanism of sensitivity to sensory stimulation as proposed by Gray (1990) offers one possible explanation for the previously discussed empirical findings. Another viable hypothesis is operation of selective attention. When organisms are confronted with two or more simultaneous stimuli, they may focus on one while disregarding the other. In a similar vein, the responsiveness of the organism may result from their divided attention, a situation in which attention is distributed among more than one of the competing sources of stimulation. In other words, the presence of one stimulus may distract from the presence of a second stimulus. Whether these mechanisms act independently of one another or in conjunction with one another is an area that requires further exploration.

In light of this notion of organisms differential responding 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 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 exceed 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 altered each hour, with the eggs rotating clockwise for an hour then rotating counter-clockwise 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 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. 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, 1991). 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 (1991) required ducklings to learn a species-atypical maternal call, whereas Lickliter and Hellewell exposed the bobwhite quail to a species-typical maternal call. Similar to the arousal based hypothesis proposed by Gray, 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, where 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 (under review) 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 confined to 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 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, chicks which received prenatal visual stimulation in a social setting preferred the bobwhite hen over the scaled hen by 24 hr of age (Lickliter, 1990a).

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 24-30 hr prior to hatching. These birds failed to show a preference for the familiar maternal call at 24 hr of age. 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 were incubated in isolation and received exposure to an individual maternal call and 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 both 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 manipulated sources, appears to have direct effects 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, 1991, 1993). Stimulation that falls within some optimal range seems to maintain or facilitate normal patterns of perceptual functioning (Lickliter, 1990a; Lickliter & Stoumbos, 1991). On the other hand, attenuated stimulation appears to interfere with normal patterns of perceptual functioning (Gottlieb, 1993; Lickliter & Lewkowicz, under review). More important for the present study is the finding that substantial increases in stimulation to an earlier developing modality can interfere with perceptual functioning of later developing systems (Krutchkoff & Lickliter, in preparation; Radell & Gottlieb, 1992). This leaves unanswered the question of how substantial increases in stimulation to a <u>later</u> developing modality will impact earlier developing systems. Equally important to this study, previous research suggests that increased amounts of stimulation can interfere with prenatal auditory learning (Gottlieb, Tomlinson & Radell, 1988; Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992). Interestingly, in these studies intersensory interference occurred only when increased cross-modal stimulation was presented concurrently. Non-concurrent stimulation or low levels of concurrent stimulation facilitated auditory learning. What remains to be explored is the effect of substantial increases in the amount of <u>non-concurrent</u> stimulation on the capacity for prenatal auditory learning.

The present study thus examined the effect of substantial increases in amount of stimulation of a later developing modality (visual) on an earlier developing modality (auditory). In a similar vein, this study also examined the effect of substantially increasing amounts of non-concurrent visual stimulation on the ability of quail embryo to learn an individual maternal call in the period prior to hatching. It was hypothesized that if this substantially increased amount of prenatal visual stimulation is not optimal for responding to unusually early visual stimulation, then chicks would show an interference in species-typical development. Finally, this study assessed the behavioral arousal level of embryos exposed to substantially increased amounts of prenatal visual stimulation in an effort to determine if arousal is a mediating factor in their subsequent postnatal perceptual responsiveness to maternal auditory and visual cues.

Hypotheses and Predictions

Previous studies have shown that quail chicks which receive 10 min/hr of patterned visual experience during the last 24-36hr of incubation exhibit a decline in species-typical auditory responsiveness and an acceleration in species-typical visual responsiveness during the days following hatching (Lickliter 1990a,b). In the present study, embryos received substantially increased amounts of unusually early visual experience prior to hatching. Specifically, subjects received four times as much visual stimulation as chicks in previous experiments. If substantially increasing visual stimulation interferes with early perceptual development, then the chicks in this study should show patterns of auditory and visual responsiveness different from both control chicks and chicks exposed to only 10 min/hr of premature visual stimulation in previous studies. Because of their substantially increased levels of prenatal stimulation, experimental chicks were expected to show functional deficits (retardation) in their subsequent postnatal perceptual responsiveness to maternal auditory and visual cues and in their ability for prenatal auditory learning.

General Method

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

Subjects

Subjects were 158 incubator-reared bobwhite quail chicks (Colinus virginianus). Fertile, unincubated eggs were received weekly from a single commercial supplier and set in a Petersime Model I incubator, maintained at 37.5 degrees Celcius and 80 to 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.

Procedure

After hatching, subjects were reared in groups of 10 to 12 same-aged chicks to mimic naturally occurring brood conditions. As a result of their incubation rearing, the only sounds to which embryos and hatchlings were exposed until the time of experimental manipulation or testing were 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 was illuminated by a 100-W brooder lamp suspended above plastic rearing tubs, which maintained an ambient air temperature of approximately 30 degrees Celcius.

To ensure that the embryos could see the unusually early visual stimulation, during the second half of the 21st day of incubation (21 day, 1200-1600 hr), 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 embryo 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, 10 to 12 opened eggs were placed in a portable, Hovi-bator incubator. Temperature and humidity were maintained as during earlier incubation.

Embryos were stimulated with a 15-W light pulsed at 3 cycles per second (maximum flash energy = 4-W sec) for 20 min each half hour during the last 24 to 30 hr prior to hatching, with 10 min rest periods in between bouts of stimulation (total exposure time = approximately 900 min). This temporally patterned light was located immediately above the Plexiglas top of the incubator, with particular care taken to ensure that the presence of the light did not alter the ambient air temperature or relative humidity within the incubator. This stimulation procedure resulted in subjects receiving substantial amounts of unusually early visual stimulation during the last 24 to 30 hr prior to hatching. Although the precocial avian embryo is responsive to prenatal visual stimulation (Heaton, 1973; Oppenheim, 1968), the embryo does not ordinarily experience patterned visual stimulation until after hatching from the egg.

Testing

Testing occurred at 24 hr, 48 hr, or 72 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 are lined with foam to attenuate echoes, and the floor is painted flat black. Two rectangular approach areas (32 X 15 cm) are demarcated on opposite sides of the arena by green strips painted on the floor. These approach areas make 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 is 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 stopwatches 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 were 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. If a subject did not enter an approach area, it received a score of 300 s for latency (the length of the trial) and 0 s for duration for that stimulus. If a chick 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, a preference for that stimulus was scored. A bird 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 experimental groups.

Data Analysis

The data of primary interest in each experiment were the measures of preference (as scored by latency and duration) for one or the other stimulus presented during a trial. Three such measures were analyzed: (1) 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, (2) differences in the duration of response to each stimulus by a subject in a group was evaluated by the Wilcoxon matched-pairs signed-ranks tests, and (3) 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 the chi-square test. Significance levels of $p < .05$ were used to evaluate results and all tests were two-tailed.

Experiment 1: Effects of Substantially Increased Prenatal Visual Stimulation on Postnatal Auditory Responsiveness

Previous studies have demonstrated that bobwhite quail chicks initially direct their social preferences on the basis of available auditory cues. Specifically, chicks show a naive auditory preference for the bobwhite maternal call over species-atypical maternal calls at both 24 and 48 hr following hatching (Lickliter & Virkar, 1989). By 72 hr of age, chicks require combined maternal auditory and maternal visual cues to direct social preference (Lickliter, 1994; Lickliter & Virkar, 1989). In contrast to unmanipulated birds, chicks exposed to unusually early visual experience for 10 min/hr during the last 24-30 hr of incubation do not demonstrate a preference for the bobwhite maternal call at either 24 or 48 hr following hatching (Lickliter, 1990a). Rather, these chicks demonstrate accelerated intersensory functioning, requiring combined maternal auditory and maternal visual cues to direct their preferential responsiveness by 24 hr following hatching (Lickliter, 1990a).

The specific mechanism that mediates the acceleration of intersensory functioning following unusually early visual experience is presently unknown. It is possible that this moderate amount of early visual stimulation, in conjunction with the normally available prenatal sensory stimulation provided by broodmates, falls within a range of stimulation that is optimal for the organisms attending and responding to the premature visual stimulation. To explore what impact substantially increasing the amount of prenatal visual stimulation would have on subsequent auditory responsiveness, this experiment provided embryos with 40 min/hr of prenatal stimulation and subsequently assessed their postnatal responsiveness to the bobwhite maternal call. If substantially increased prenatal stimulation serves to interfere with hatchlings' early perceptual functioning, then birds receiving these greatly augmented amounts of visual stimulation as embryos should demonstrate a postnatal pattern of responsiveness to maternal auditory cues different from that seen in chicks receiving no visual stimulation (Lickliter & Virkar, 1989) or only moderate amounts of prenatal visual stimulation (Lickliter, 1990a). Specifically, a substantial increase in prenatal visual stimulation should decrease an organism's attentiveness and responsiveness to the prenatal visual stimulation, thereby interfering with typical patterns of postnatal auditory functioning.

Method

Sixty bobwhite quail embryos, drawn from eleven 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 40 min per hour for a minimum of 24 hr from the second half of Day 21 (1200-1600 hr) to the second half of Day 22 of incubation with a 15-W light pulsed at 3 cycles per second (see General Method). This patterned visual stimulation was presented in 20 min burst, with 10 min between stimulation sessions, to reduce the likelihood of possible habituation effects. To determine if this prenatal manipulation affected hatchlings' species-typical auditory preference for the maternal call, subjects were given a simultaneous-choice test between a bobwhite maternal call and a chicken maternal call at either 24 hr after hatching (n = 20), 48 hr after hatching (n = 20) or 72 hr after hatching (n=20). 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. Choice, latency, and duration of response were collected and analyzed as described in the General Methods section.

Results and Discussion

The results of Experiment 1 are shown in Tables 1 and 2. Chicks exposed to the substantially increased amount of prenatal visual stimulation 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). 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). Specifically, chicks in this experiment did not respond to the chicken maternal call, indicating that this particular sensory experience appears to have erased any variability in responsiveness at the level of the individual.

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 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 hr following hatching. In the present experiment, chicks continued to demonstrate a preference for the bobwhite maternal call at 72 hr following hatching, indicating an altered pattern of species-typical auditory functioning.

The findings of the present experiment also stand in contrast to results obtained from a previous experiment in which embryos were exposed to 10 min/hr of prenatal visual stimulation (Lickliter 1990a). Chicks in that experiment did not demonstrate a preference for the bobwhite maternal call at either 24 or 48 hr following hatching. Rather, these chicks exposed to 10 min/hr of prenatal visual stimulation demonstrated accelerated intersensory functioning, requiring combined maternal auditory and maternal visual cues to direct their preferential responsiveness by 24 hr following hatching (Lickliter, 1990a). In other words, providing embryos with moderately augmented amounts of visual stimulation accelerated intersensory functioning. In the present experiment, chicks exposed to 40 min/hr of prenatal visual stimulation did not exhibit this accelerated pattern of intersensory functioning, suggesting that substantially increasing the amount of prenatal visual stimulation experienced by an embryo may lead to delayed intersensory development. Taken together, these results seem to suggest that moderate increases in amount of prenatal stimulation may accelerate species-typical intersensory functioning, whereas substantial increases in amount of prenatal stimulation may result in deficits in species-typical intersensory functioning. The purpose of the next experiment was to investigate whether the effects found in Experiment 1 would generalize to responsiveness in other sensory systems by examining the effect of substantially increased amounts of prenatal visual stimulation on chicks' postnatal visual responsiveness to maternal cues.

Experiment 2: Effects of Substantially Enhanced Prenatal Visual Stimulation on Postnatal Species-Specific Visual Responsiveness

Previous studies have demonstrated that bobwhite quail chicks show a naive visual preference for a bobwhite hen model over a scaled quail hen model when both hens are emitting the same bobwhite maternal call by 72 hr following hatching (but not at earlier ages; Lickliter & Virkar, 1989). In contrast to unmanipulated birds, chicks exposed to unusually early visual experience for 10 min/hr during the last 24-30 hr prior to hatching demonstrate a preference for the bobwhite hen over the scaled quail hen (when both are emitting the same bobwhite maternal call) by 24 hr following hatching (Lickliter, 1990b). It is important to note that the static visual cues provided by the hen models alone are not sufficient to elicit preferential responsiveness at any ages tested. Rather, maternal visual cues must be presented with the maternal call to be effective in directing social preferences (Lickliter & Virkar, 1989).

To explore what impact substantially increased amount of prenatal visual stimulation might have on auditory/visual responsiveness, this experiment provided embryos with 40 min/hr of prenatal stimulation and subsequently assessed their postnatal responsiveness to species-typical maternal auditory and visual cues. If substantially increased amounts of prenatal stimulation interferes with hatchlings' early perceptual functioning, then birds receiving increased amounts of visual stimulation as embryos should demonstrate a postnatal pattern of responsiveness to maternal auditory/visual cues different from that seen in chicks receiving no visual stimulation (Lickliter & Virkar, 1989) or only moderate amounts of prenatal visual stimulation (Lickliter, 1990b). Specifically, if substantially increased stimulation decreases embryos' attentiveness and responsiveness to unusually early visual stimulation, then chicks exposed to these substantially increased amounts of visual stimulation should not demonstrate the postnatal acceleration of the emergence of intersensory integration observed in chicks exposed to mildly enhanced levels of prenatal visual stimulation in previous studies.

Method

Sixty bobwhite quail embryos, drawn from ten separate hatches, served as subjects. All birds were embryonically stimulated as described in Experiment 1. Subjects were tested at either 24 hr, 48 hr, or 72 hr after hatching. During these 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 and a stuffed model of a species-atypical scaled quail hen (*Calipepla squamata*). In other words, during testing both hen models were emitting the same species-typical bobwhite maternal call, requiring subjects to direct their social preference of the basis of available static visual cues, because the available auditory cues (identical maternal calls) did not allow a basis for decision. Choice, latency, and duration of response were scored and analyzed as described in the General Methods section.

Results and Discussion

The results of testing are illustrated in Tables 3 and 4. Chicks did not show a preference for either hen model at any ages tested. Correspondingly, there were no significant differences in the subjects' latency and duration scores for either of the stimuli presented during testing.

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. In the present experiment, chicks failed to demonstrate a preference for the bobwhite maternal auditory/visual cues at any age tested, indicating interference with the species-typical pattern of intersensory development.

The findings of the present experiment also stand in contrast to results obtained from a previous experiment in which embryos were exposed to 10 min/hr of prenatal visual stimulation (Lickliter, 1990a). These chicks demonstrated accelerated intersensory functioning, requiring combined maternal auditory and maternal visual cues to direct their preferential responsiveness by 24 hr following hatching. In other words, providing embryos with moderately augmented amounts of visual stimulation accelerated intersensory functioning. In the present experiment, chicks exposed to 40 min/hr of prenatal visual stimulation did not exhibit this accelerated intersensory functioning, suggesting that substantially increasing the amount of prenatal visual stimulation experienced by an embryo leads to delayed intersensory development. This experiment provides further evidence that moderate increases in amount of prenatal stimulation may accelerate species-typical intersensory functioning, whereas substantial increases in amount of prenatal stimulation may result in deficits in species-typical intersensory functioning.

In particular, the findings of Experiments 1 and 2 suggest that substantially increased amounts of unusually early visual experience result in altered postnatal auditory and visual functioning. In both experiments, birds showed postnatal perceptual behavior that was temporally retarded when compared to unmanipulated birds. As previously suggested, these birds may not have attended to the relevant aspects of their prenatal environment necessary for species-typical perceptual development. If the hypothesis of a generalized mechanism which responds to amount of stimulation is true, then substantially increasing the amount of prenatal visual stimulation should adversely affect embryos' sensitivity to prenatal auditory stimulation as well. In other words, the experience of substantially increased amounts of visual stimulation should prevent embryos from attending to auditory stimulation present in the prenatal environment. The purpose of the next experiment was to examine this possibility.

Experiment 3: Effects of Substantially Enhanced Prenatal Visual Stimulation on Prenatal Auditory Learning

Previous research has shown that socially incubated bobwhite quail embryos can learn an individual bobwhite maternal call and remember that familiar call for at least 24 hr following exposure (Lickliter & Hellewell, 1992). Specifically, embryos exposed to a particular variant of the bobwhite maternal call during the later stages of incubation subsequently demonstrate an auditory preference for that call over another unfamiliar bobwhite maternal call when tested postnatally (Lickliter & Hellewell, 1992). Embryos exposed to 10 min/hr of non-concurrent prenatal visual stimulation and the maternal call also demonstrate this auditory learning ability (Lickliter & Hellewell, 1992).

This experiment examined the affect of substantial increases in the amount of visual stimulation on prenatal auditory learning. If substantially increasing the amount of prenatal stimulation presented to embryos results in altered sensitivity to prenatal stimulation, then experimental birds should show deficits in their ability to learn an individual maternal call prenatally.

Method

Twenty bobwhite quail embryos, drawn from three separate hatches, served as subjects. The experimental procedures of the previous two experiments were repeated, with the exception that in this experiment subjects also received non-concurrent exposure to an individual bobwhite maternal call (Call B) for one of the 10 min periods each hour that they were not receiving visual stimulation. In other words, subjects received 40 min of unusually early visual stimulation and 10 min of auditory stimulation each hour. This auditory stimulation began on the second half of the 21st day of incubation and continued through the second half of the 22nd day of incubation. Total prenatal auditory stimulation with the maternal call amounted to approximately 4 hr. The recording of the individual maternal call was broadcast to the embryos through a Marantz Model PMD 221 cassette recorder and presented at a peak intensity of 65 dB, as measured by a Bruel & Kjaer Model 2232 sound level meter. All the normally occurring acoustic components of the maternal vocalization were present and unaltered. Following hatching, subjects were reared socially with 10-12 same-aged chicks until testing at 24 hr of postnatal age. During testing, individual subjects were given a simultaneous choice test between the familiar bobwhite maternal call (Call B) and an unfamiliar variant of the bobwhite maternal call (Call A). These two maternal calls were recorded in the field and are similar in phrasing, call duration, repetition rate, dominant frequency, and frequency modulation (see Table 1, Heaton, Miller, & Goodwin, 1978). The sound intensity of both of the calls peaked at 65 dB at the point where the chick was introduced into the test arena. Choice, latency, and duration of response were scored as described in the General Methods section.

Results and Discussion

The results of this experiment are illustrated in Tables 5 and 6. Chicks failed to demonstrate a significant preference for the familiar bobwhite maternal call over the unfamiliar bobwhite maternal call at 24 hr following hatching. Analysis of the latency and duration scores further supported these results, with no significant differences between the scores associated with the two auditory stimuli.

These findings stand in contrast to results obtained from unmanipulated chicks in a previous experiment (Lickliter & Hellewell, 1992). In the Lickliter and Hellewell (1992) study, embryos exposed to a particular variant of the bobwhite maternal call during the later stages of incubation subsequently demonstrated an auditory preference for that call over another unfamiliar bobwhite maternal call when tested postnatally. In addition, embryos exposed to 10 min/hr of non-concurrent prenatal visual stimulation and the maternal call also preferred the familiar call in postnatal testing, indicating the prenatal visual experience in and or itself does not necessarily interfere with prenatal auditory learning (Lickliter & Hellewell, 1992).

Research with other precocial bird species also supports the finding that auditory learning ability varies depending on the amount of stimulation to which the organism is exposed. As previously discussed, Gottlieb et al (1989) found that unmanipulated mallard duckling 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. Embryos provided non-concurrent visual stimulation and exposure to the individual maternal call also demonstrate a preference for the familiar call over an unfamiliar one. 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. Taken together, these results suggest that substantially increasing the amount of stimulation an embryo encounters somehow decreases the organism's sensitivity to stimulation present in the prenatal environment.

An important step in understanding the effects of substantially increased prenatal visual stimulation on perceptual organization is to explore the possible mechanisms involved. As previously suggested, one explanation for changes in perceptual responsiveness as a result of manipulations of sensory stimulation is changes in the 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.

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 vocalization, 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 emit distress calls during the first 72 hr following hatching and do not exhibit species-typical responsiveness to auditory/visual maternal cues at 72 hr of age. 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). The next experiment used prenatal vocalizations as a behavioral measure of arousal level to compare control chicks, which had undergone the egg opening procedure but received no augmented sensory stimulation, and experimental chicks, which had received greatly augmented amounts of prenatal visual stimulation in the period prior to hatching.

Experiment 4: Prenatal Observations of Chicks Receiving Early Head Exposure Without Prenatal Visual Stimulation and With Prenatal Visual Stimulation

To provide a control condition, this experiment first examined the number of prenatal vocalizations emitted by embryos which had undergone the egg-opening procedure but did not receive enhanced visual stimulation prior to hatching. The behavior of these control embryos was then compared to embryos exposed to 40 min/hr of prenatal visual stimulation during the late stages of incubation.

Method

Thirty-six chicks, drawn from six different batches (i.e., weeks), 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 6 same-aged embryos. Three of the groups received no prenatal visual stimulation (total n = 18), while three of the groups received 40 min/hr of prenatal visual stimulation (total n = 18). Each group of 6 embryos was observed and their vocalizations recorded by means of a Bruel and Kjaer Type 2633 microphone connected to a Tascam model 122 cassette tape recorder. Recordings were made during three 10 min intervals, once at 12 hr after the egg opening procedure, once at 16 hr after the the egg opening procedure and once at 20 hr after the egg opening procedure. Each of the three 10 min intervals of assessment were divided into two 5 min segments. For the experimentally manipulated embryos, the first 5 min assessment period corresponded with a non-stimulation period and the second 5 min assessment period corresponded with a visual stimulation period. (The first 5 min segment of the control group was compared to the first 5 min segment of the experimental group. The second 5 min segment of the control groups was compared to the second 5 min segment of the experimental group.) Audio recordings were analyzed aurally and the number of distress vocalizations emitted for each group was scored. Previous observations with bobwhite quail chicks reveal that chicks suppress their own vocalizations while attending to other chicks' vocalizations and alternately respond with their own distress calls (McBride & Lickliter, 1993,1994). This finding of alternating calls is consistent with previous findings obtained from ducklings (Gaioni, 1982; Gaioni & Platte, 1982). A minimum of two raters was used to assess and score the vocalizations of each group, affording a measure of interobserver reliability (r = .99).

To evaluate the statistical reliability of within-group differences between the nonstimulation and stimulation period, three Wilcoxon Signed-Ranks tests were employed (see Figure 1). These tests specifically take into account the direction of change and magnitude of change in vocalizations. If the direction of change is 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 share a certain direction of change, the magnitude of the majority's change must be large and the magnitude of change in the minority's performance must be relatively small. Since there are likely to be individual variation in vocalization rates, the Wilcoxon tests seemed particularly appropriate in the present context. Because there were differences in the amount of stimulation experienced in the two time periods, it was hypothesized that there would be significant differences in the number of vocalizations emitted during these periods.

Similarly, within-group differences between the 5 min segments of control birds were evaluated with three Wilcoxon Signed-Ranks tests. These nonparametric tests compared each embryo's performance in the first 5 min segment with its performance in the second 5 min segment at each of the three time periods. Because there were no differences in stimulation, it was hypothesized that there would be no significant difference in number of vocalizations emitted during the four time samples.

Results and Discussion

The within-group results of this experiment are shown in Table 3. No statistically significant difference was found in number of vocalizations between the nonstimulation and stimulation period of experimental birds. Similarly, no significant difference was found in number of vocalizations between the first 5 min assessment period and the second 5 min assessment period of control birds. The lack of significant findings suggests that either 1) there are no actual differences between the time periods or that 2) the data trends were too subtle to be detected with the statistics employed. In fact, it is likely that the statistical tests employed were not powerful enough to detect any differences due to the limited number of data points. Also, the high within-group variability for the experimental group may have masked any systematic between-group differences.

Because there were no within-group differences between cells in either the control or experimental groups, the number of vocalizations in each 5 min segment were combined into a total number for the 10 min assessment period. The next step was to examine any within-group differences between the three times of assessment. Six Wilcoxon Signed-Ranks tests were employed to compare time periods within each condition, either control or experimental (see Figure 1). The results of this test are shown in Table 3. No statistically significant differences were found between each of the three time periods within each condition. For example, the number of vocalizations for the experimental group did not differ between 12, 16, or 20 hr following opening. These findings suggest that there are no age effects and that the effect of visual stimulation is not cumulative.

Because there were no within-group differences between time periods in either the experimental or control groups, the mean number of vocalizations was calculated for each condition. An independent t-test was employed to examine any between-group differences on the two means (see Figure 1). Results of this test are shown in Table 3. No statistically significant difference was found between the mean number of vocalizations for the control group and the mean number of vocalizations for the experimental group. The lack of significant findings suggests that either 1) there are no actual differences between the two, or that 2) the data trends were too subtle to be detected. In fact, the raw data indicates that there may indeed be differences between the experimental group (mean # of vocalizations = 23.56) and the control group (mean # of vocalizations = 4.78), but in the present experiment there were not enough data points to adequately assess this conclusion. While no significant differences between the number of vocalizations of the control and experimental birds were found, the high degree of variability evident in the experimental group may have conceptual significance. That is, the large difference between the means suggests that the experimental birds did indeed differ in some manner from the control birds. Specifically, the experimental birds demonstrated a high degree of variability in their responsiveness, whereas the control birds maintained a consistent pattern of responsiveness over the course of the assessment periods.

In an effort to further explore this possibility, an independent t-test was employed to examine any between-group differences in variability. Specifically, the average standard deviation of the experimental group was compared to the average standard deviation of the control group. No statistically significant differences were found. However, the means of the standard deviations did show trends similar to those found with the means of number of vocalizations (mean of standard deviations for experimental group = 33.02; mean of standard deviations for control group = 2.06). As previously discussed, these findings may have conceptual significance in that the difference in the means suggests that the experimental birds appear to have more variation in responsiveness than do control birds. To adequately assess this conclusion, however, a greater number of data points will need to be collected and analyzed.

General Discussion

This study examined whether previously reported effects of altered prenatal sensory experience on subsequent acceleration of intersensory functions are mediated by mechanisms sensitive to the overall amount of stimulation. This was done by varying the amount of visual stimulation provided quail embryos during the last stages of incubation to determine whether increasing overall amount of visual stimulation would modify subsequent intersensory development. Results revealed that chicks exposed to substantially augmented prenatal visual experience show interference in subsequent species-typical perceptual development. Specifically, chicks continued to respond to maternal auditory cues into later stages of postnatal development (Experiment 1) and failed to respond to maternal visual cues at the age when normally reared chicks exhibit this species-specific ability (Experiment 2). The findings from Experiment 1 and 2 stand in contrast to results previously obtained from chicks exposed to 10 min/hr of prenatal visual stimulation, in that chicks exposed to 10 min/hr of prenatal visual stimulation show accelerated intersensory functioning during the days following hatching. Embryos exposed to substantially augmented visual stimulation in this study also failed to demonstrate early auditory learning of an individual maternal call (Experiment 3), a behavior reliably seen in unmanipulated embryos and embryos exposed to 10 min/hr of visual stimulation.

These results underscore the dynamic nature of early perceptual organization in precocial birds. Stimulation that falls within some optimal range seems to maintain or facilitate normal patterns of perceptual functioning (Lickliter, 1990a; Lickliter & Stoumbos, 1991; Radell & Gottlieb, 1992). On the other hand, substantially attenuated or substantially increased amounts of stimulation appear to prevent the emergence of species-typical patterns of intersensory functioning (Gottlieb, 1993; Lickliter & Lewkowicz, under review), and can also interfere with prenatal auditory learning (Gottlieb et al, 1988; Lickliter & Hellewell, 1992; Lickliter & Lewkowicz, under review; Radell & Gottlieb, 1992).

These studies demonstrating interference in auditory learning ability potentially provide insight into how avian embryos respond to concurrent multimodal stimulation versus non-concurrent multimodal stimulation during prenatal development. Recall that experiments which provide embryos with levels of stimulation which mildly exceed that experienced under normal conditions found that intersensory interference occurred only when cross-modal stimulation was presented <u>concurrently</u>. Non-concurrent stimulation or very low levels of concurrent stimulation served to allow auditory learning (Gottlieb et al, 1989; Lickliter &

Hellewell, 1992). The present experiment demonstrated that substantially increasing the amount of non-concurrent stimulation also results in deficits in prenatal auditory learning. Taken together, these findings suggest that the effects of prenatal sensory stimulation are not necessarily cumulative. In other words, 10 min/hr of visual stimulation followed by 10 min/hr of auditory stimulation is not perceived the same by the embryo as 10 min/hr of visual stimulation and 10 min/hr of auditory stimulation presented concurrently.

The picture is further complicated by results from research that reared embryos with levels of stimulation which were less than that experienced under normal conditions. For example, Lickliter & Lewkowicz (under review) found that embryos incubated under conditions which attenuated normal levels of vestibular and proprioceptive stimulation failed to demonstrate early auditory learning of an individual maternal call, whereas isolate reared embryos receiving visual stimulation concurrently with exposure to an individual maternal call did demonstrate prenatal auditory learning. In other words, embryos required the increased amount of stimulation (presented concurrently) to compensate for the attenuated amount of stimulation rendered by physical isolation during incubation. Taken together, these experiments suggest that there is no predictable perceptual outcome based solely on stimulation being concurrent or non-concurrent. Rather, the developmental history and current state of the organism must also be taken into consideration.

Under normally occurring conditions, the structured developmental system provided by the egg serves to reduce the possible degrees of freedom contributing to early perceptual organization. Specifically, limits in the amount of sensory stimulation experienced during development provides an orderly structure for the developing embryo that is essentially similar across members of a species. These limits, in turn, influence the nature of intersensory relationships in the perinatal period. This notion of an orderly context for development is consistent with a view of development that recognizes that the organism-environment relationship is one that is structured on both sides. That is, there is a relationship between a structured organism and a structured environment (Lickliter, 1993). As the previous discussion of results attempts to make clear, 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 uniquely constructed during the course of each individual's development. Similarities are seen at the group level because the structured nature of the organism-environment relationship renders relatively similar experiential histories among members of a given species.

To gain a clearer understanding of how perceptual development is constructed, this relationship between the organism and its developmental context must be explored more thoroughly. 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 tests 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 alter their subsequent visual stimulation preference.

Although the studies discussed above provide useful descriptive information regarding potential arousal effects on perception, future studies need to focus on identifying and explaining the underlying mechanisms that mediate perception. Specifically, the arousal level and attentional capacities of the organism in its developmental context should be more thoroughly explored. As previously discussed, behavioral measures such as number of vocalizations may be too crude of a measure to adequately assess arousal level in precocial avian species. Consequently, a broader base of behavioral and physiological probes aimed at assessing the arousal and attentional features of intersensory development need to be utilized.

Previous research also raises the issue that the range of stimulation that is considered optimal may shift depending on the context in which it occurs. One example of this shift is differential responsiveness based on task difficulty. Recall that Gottlieb (1991) found that duckling hatchlings reared in isolation failed to learn a non-conspecific chicken maternal call, whereas Lickliter and Hellewell (1992) demonstrated that bobwhite quail hatchlings reared in social isolation did exhibit the ability to learn a species-typical bobwhite maternal call. These conflicting results may result from the complexity of the two tasks. Gottlieb (1991) required ducklings to learn a species-atypical maternal call, while Lickliter and Hellewell (1992) required quail hatchlings to learn a species-typical maternal call. These findings suggest that the arousal level that is optimal for learning may shift as a function of task difficulty (Gray, 1990). Future studies should continue to unpack this nested relationship between amount of stimulation and the context in which it occurs.

Finally, the <u>type</u> of stimulation experienced may be an important factor in determining what is an optimal range of stimulation for the young organism. For example, McBride and Lickliter (1994) found that bobwhite hatchlings exposed to bobwhite chick contentment calls, domestic chicken hatchling distress calls, or no augmented auditory stimulation exhibited species-typical auditory and visual responsiveness to maternal cues, whereas bobwhite hatchlings exposed to bobwhite chick distress calls do not exhibit this species-typical behavior. These results suggest that specific types of postnatal auditory stimulation, rather than simply increased amount of stimulation, may be necessary to interfere with species-typical intersensory functioning. What remains to be explored is whether the interference in species-typical perceptual functioning caused by certain types of stimulation (in this case, bobwhite chick distress calls) also holds during prenatal development and whether such interference can be ameliorated by reducing the amount of stimulation provided. In other words, future studies should also address the question of how the optimal range of stimulation interacts with the type of stimulation provided to more fully unpack the heirarchies of influence involved in early perceptual organization.

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

Age (in hrs)	n	n responding	Preference: Bobwhite Maternal Call	Chicken Maternal Call	No Preference
24	20	20	20*	0	0
48	20	17	17*	0	0
72	20	19	19*	0	0

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

Table 2. Means and Standard Deviations of Latency and Duration Scores of Chicks in Simultaneous Auditory Choice Tests in Experiment 1.

		Latency		Duration	
Age (in hrs)	n	Bobwhite Maternal Call	Chicken Maternal Call	Bobwhite Maternal Call	Chicken Maternal Call
24	20	43.85* (40.56)	300 (0)	167.9* (55.84)	0 (0)
48	20	61.45* (104.22)	300 (0)	125.4* (90.94)	0 (0)
72	20	40.7* (66.02)	300 (0)	90.35* (44.22)	0 (0)

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

Table 3. Preference of Chicks in Simultaneous Auditory-Visual Choice Tests in Experiment 2.

Age (in hrs)	n	n responding	Preference: Bobwhite Hen with Bobwhite Maternal Call	Scaled Hen with Bobwhite Maternal Call	No Preference
24	20	19	9	4	6
48	20	19	9	6	4
72	20	18	10	3	5

Table 4. Means and Standard Deviations of Latency and Duration Scores of Chicks in Simultaneous Auditory-Visual Choice Tests in Experiment 2.

		Latency		Duration	
Age (in hrs)	n	Bobwhite Hen with Bobwhite Maternal Call	Scaled Hen with Bobwhite Maternal Call	Bobwhite Hen with Bobwhite Maternal Call	Scaled Hen with Bobwhite Maternal Call
24	20	87.25 (112.02)	104.30 (121.85)	93.75 (79.76)	55.85 (56.13)
48	20	71.15 (99.85)	64.65 (71.50)	76.55 (60.62)	69.80 (61.56)
72	20	91.4 (97.42)	119.3 (125.40)	71.80 (59.23)	31.55 (41.19)

Table 5. Preference of Chicks in Simultaneous Auditory Learning Choice Tests in Experiment 3.

			Preference		
Age (in hrs)	n	n responding	Bobwhite Maternal Call A	Bobwhite Maternal Call B	No Preference
24	20	19	7	3	9

Table 6. Means and Standard Deviations of Latency and Duration Scores of Chicks in Simultaneous Auditory Learning Choice Tests in Experiment 3.

		Latency		Duration	
Age (in hrs)	n	Bobwhite Maternal Call A	Bobwhite Maternal Call B	Bobwhite Maternal Call A	Bobwhite Maternal Call B
24	20	73.70 (101.45)	82.90 (81.44)	71.70 (53.13)	61.30 (69.93)

Table 7. Means and Standard Deviations of Number of Vocalizations of Chicks in Experiment 4.

Chicks Exposed to 40 min/hr Prenatal Visual Stimulation						Chicks Undergoing Egg-Opening Procedure					
12 hr post opening		16 hr post opening		20 hr post opening		12 hr post opening		16 hr post opening		20 hr post opening	
non-stim	stim	non-stim	stim	non-stim	stim	1st half	2nd half	1st half	2nd half	1st half	2nd half
1.33 (1.53)	5 (4)	42.6 (73.9)	2 (2)	17.7 (20.8)	2 (1.73)	1.67 (1.15)	1.33 (1.15)	4.33 (4.04)	2.67 (1.15)	1.67 (0.58)	2.67 (1.15)
6.33 (4.73)		44.67 (73.93)		19.67 (20.40)		3 (2)		7 (3.61)		4.33 (.58)	
23.5556 (41.95)						4.7777 (2.73)					

Figure 1: Statistical phases of analysis in Experiment 4.

Six Wilcoxon Signed-Ranks tests were employed to compare each group's performance in the first 5 min segment with its performance in the second 5 min segment at each of the three time periods. For the experimental group, these tests compared the groups performance in a nonstimulation period with their performance in a stimulation period.

EARLY VISUAL STIMULATION
(hrs after onset of stim)
12 16 20

CONTROL GROUP
(hrs after egg opening)
12 16 20

Because there were no differences within-group between the first and second 5 min time blocks, six Wilcoxon Signed-Ranks tests were employed to compare time periods within each condition.

EARLY VISUAL STIMULATION
(hrs after onset of stim)
12 16 20

CONTROL GROUP
(hrs after egg opening)
12 16 20

Because there were no within-group differences between time period in either the experimental or control groups, the number of vocalizations were collapsed across conditions and an independent t-test was employed to examine any between-group differences on the two means.

EARLY VISUAL STIMULATION
(hrs after onset of stim)
12 16 20

CONTROL GROUP
(hrs after egg opening)
12 16 20

MERRY J. SLEIGH

CURRENT ADDRESS:

Home: 401 Fairfax Road
Apt. 631
Blacksburg, VA 24060
Phone: (703) 552-1255

Office: Psychology Dept.
Virginia Polytechnic
Institute and State
University
Blacksburg, VA 24061
Phone: (703) 231-6279

EDUCATION:

1992-1994 M.S. in Developmental Psychology
Virginia Polytechnic Institute and
State University, Blacksburg, VA

1988-1992 B. A. in Psychology/English
Summa Cum Laude
James Madison University
Harrisonburg, VA

TEACHING EXPERIENCE:

1992-93 Graduate Teaching Assistant, Introductory Psychology, VPI & SU, Blacksburg, VA
Instructed lab sessions of introductory psychology course. Developed lectures, exercises, and presentations to facilitate class discussion. Provided individual assistance to students.
Supervisor: Joseph Sgro, Ph.D

WORK EXPERIENCE:

1993-94 <u>Lab Manager/Graduate Research Assistant</u>

VPI & SU, Blacksburg, VA

Responsible for management of psychobiology research lab. Coordinated undergraduate research assistants and ongoing research projects.

Supervisor: Robert Lickliter, Ph.D

1991-92 <u>Undergraduate Hall Director</u>

James Madison University, Harrisonburg, VA

Selected, trained and provided individualized supervision for staff of resident advisors. Advised Hall Council. Handled disciplinary and referral situations Designed and implemented programming to address women's issues. Responsible for residence hall of over 200 upperclass women.

Supervisor: James McConnel

1990-91 <u>Assistant Hall Director</u>

James Madison University, Harrisonburg, VA

Supervised staff of fifteen resident advisors Planned and facilitated staff meetings. Advised Hall Council. Conducted discipline and mediation meetings and monitored programming. Responsible for the coeducational living environment of over 400 first year students.

Supervisor: James McConnel

1989-92 Assistant Coordinator - Compeer

Harrisonburg, VA

Assisted in assessing status of client/volunteer relationships. Promoted awareness of mental illness in community.

Supervisor: Donna Shickel

Volunteer - Compeer

Matched in one-to-one relationship with two mental health patients. Assisted in the successful rehabilitation and re-entry of the mentally ill into the community by providing individual support. Assisted the clients in improving their communication and social skills.

Supervisor: Donna Shickel

PAPERS PRESENTED AT SCIENTIFIC MEETINGS:

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

PROFESSIONAL SERVICE:

1993-94 Graduate Student Honor Court Representative

VPI & SU, Blacksburg, VA

1991-92 Psi Chi Treasurer, National Psychology Honor Society

James Madison University, Harrisonburg, VA

HONORS AND AWARDS:

Sigma Tau Delta, National English Honor Society

Phi Kappa Phi, National Honor Society

Golden Key National Honor Society

National Dean's List