MODIFIED POSTNATAL SOCIAL EXPERIENCE ALTERS INTERSENSORY DEVELOPMENT OF BOBWHITE QUAIL CHICKS

by

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(ABSTRACT)

Recent studies have begun to explore the features of perinatal experience which facilitate infants' abilities to integrate information from the various sensory modalities. The present study utilized a precocial avian infant, the bobwhite quail (*Colinus virginianus*), to explore 1) what types of postnatal social experience young chicks require to successfully pair sights and sounds and 2) when these experiences need to occur to maintain species-typical intersensory development. Specifically, chicks in this study were reared in one of four conditions: with normal siblings, with altered tactile experience, with altered auditory experience, or with altered visual experience. Findings revealed that altered tactile, auditory, and visual experience presented throughout the first 72 hrs of postnatal development delays chicks' ability to integrate maternal auditory and visual information at 72 hrs of age, a response reliably seen in unmanipulated chicks. Furthermore, results showed that altered sensory experience in any modality presented during the first 36 hrs of postnatal development delays intersensory responsiveness. Altered tactile or auditory sensory information presented during the last 36 hrs of postnatal development also disrupted normal perceptual development, while altered visual information presented during the last 36 hrs of postnatal development failed to disrupt species-typical responsiveness. These findings suggest that normal sensory experience derived from social interaction is important for normal species-typical development.

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Modified Postnatal Social Experience Alters Intersensory Development of Bobwhite Quail Chicks

Developmental psychologists have increasingly turned their attention to the processes and mechanisms that, over time, influence the relationship between organisms and their specific environments. Because biological systems are continually changing, rather than static, the experiences that organisms create and encounter can influence developmental processes and thus, developmental outcomes. Developmental research has demonstrated that few linear causes of subsequent behavior exist, and that instead, reliable behavioral outcomes typically result from the interdependence and interactions between multiple levels of analysis within any developing system. This dynamic approach to studying development is a viable and rapidly emerging direction of research in developmental psychology (Oyama, 1985, 1993; Thelen & Smith, 1994), as well as in evolutionary biology (Gould, 1977; Kauffman, 1995), developmental biology (Edelman, 1992), and the neurosciences (Stein & Meredith, 1993).

One fundamental principle that has emerged from contemporary developmental science is that experience plays a critical role in development for organisms of any species (Capitanio, 1984; Gottlieb, 1991b; Johnston, 1987; King & West, 1987; Lickliter, Dyer, & McBride, 1993; Lickliter & Gottlieb, 1986a, b). While some researchers continue to argue that many behaviors are innate or are caused by exclusively genetic influences, an increasing body of research has demonstrated that the experience of the organism is likewise crucial to understanding how phenotypic traits and characters emerge in development. In fact, King and West (1987) have pointed out that organisms "inherit not only genes, but also species-typical companions and habitats." From this view, the minimum unit for the developmental analysis of species-typical behavior is the developmental system, which is comprised of both the developing organism and its specific environment or context (Lickliter & Berry, 1990; Lickliter, Dyer, & McBride, 1993). Importantly, one feature common to most species-typical environments is that numerous social relationships exist between organisms present within that environment. Several researchers have argued that these social influences form the foundation for the evolutionary progression of higher psychological processes (Gottlieb, 1991a; der Veer & Valsiner, 1988).

Research examining the effects of social influence on normal development has found that differential types and amounts of social stimulation reliably change behavior in a variety of species. For example, Zajonc, Wilson, and Rajecki (1975) altered the visual appearance of different groups of domestic chicks by coloring their feathers either green or red. Experimental chicks were then reared either with similar-colored or dissimilar-colored siblings, thus creating groups of "strangers" and "companions." Findings revealed that chicks engaged in more pecking behavior when encountered with strangers than with companions, suggesting that normal pecking behavior can be changed by altering the social environment in which the chicks are reared. In a subsequent study, Rajecki, Suomi, Scott, and Campbell (1977) discovered that domestic chicks who were either 1) isolated from their siblings for three weeks or 2) separated from their siblings after two weeks and then reared in isolation, exhibited behavioral anomalies such as decreased activity levels and high levels of disturbance.

Research with other precocial bird species has also produced evidence that social influences direct developmental outcomes. Much of this evidence has emerged from studies investigating the malleability of imprinting, a filial behavior that many psychologists and biologists had historically considered innate. This tenet resulted from several lines of research which reliably demonstrated imprinting across experimental settings. However, the paradigm of these experiments mainly consisted of rearing experimental subjects in social isolation until testing (Gaioni, DePaulo, & Hoffman, 1980), which essentially constituted an experimental manipulation in itself, since imprinting does not occur in a social vacuum. Specifically, these early studies did not take into account the natural social context of the young organism, which Gottlieb (1983) and Johnston (1981) have suggested should be included in any experimental analysis of behavior.

In response to these early shortcomings in imprinting research, Johnston and Gottlieb (1985) reported that young ducklings who are allowed social experience with siblings after initial imprinting training demonstrate different visually imprinted preferences than ducklings who were reared in isolation. In a series of studies expanding on the experiential effects of the imprinting phenomenon, Lickliter and Gottlieb (1985; 1986a, b; 1987; 1988) found that, far from being an innate behavior, imprinting is in fact molded by the specific experiences that the developing organism encounters. For example, the first study in this series (Lickliter & Gottlieb, 1985) showed that if mallard ducklings are allowed social interaction with siblings in the posthatching environment, they display a preference for a mallard hen over an unfamiliar redhead hen. However, if ducklings were (a) either reared in isolation but allowed to see and hear one sibling, or (b) reared directly with one sibling, or (c) reared in a group of siblings but denied direct social interaction, no visual preference for the familiar mallard hen is demonstrated. These results suggested that social rearing experience directly influences imprinted maternal preferences.

In a similar vein, Lickliter and Gottlieb (1986a) expanded on this preliminary study by examining how the maternal imprinting phenomenon is specifically changed by social interaction with siblings. In this study, one-day-old ducklings followed a stuffed mallard hen for 30 minutes, which resulted in a visually imprinted preference for the stuffed hen over 4 stuffed ducklings at 48 and 72 hr following hatching, for ducklings who were reared in social isolation. However, if ducklings were reared with either siblings or with siblings and a stuffed mallard hen, then imprinted ducklings preferred stuffed ducklings rather than a stuffed hen at 48 and 72 hr of age. Thus, social rearing with siblings eliminated ducklings' preferences for maternal stimuli which had been previously imprinted, and demonstrated the flexibility of early perceptual responsiveness (Lickliter & Gottlieb, 1986a).

In a subsequent study, Lickliter and Gottlieb (1986b) investigated the effects of social experience <u>during</u> the maternal imprinting process. Specifically, 24 hr old chicks were allowed to follow a stuffed maternal hen for 30 minutes either alone or with a group of four same-aged siblings. Results revealed that birds in the alone condition showed an imprinted preference for the familiar mallard hen over an unfamiliar hen or four stuffed ducklings at 48 and 72 hr post-hatching. However, ducklings imprinted during the presence of siblings 1) failed to demonstrate a preference for the familiar hen over the unfamiliar hen and 2) preferred the stuffed ducklings over the mallard hen at 48 and 72 hr of age. These results demonstrate that even brief experience with siblings leads to peer imprinting and interferes with maternal imprinting, and provide further evidence of how social experience with siblings influences the development of filial preferences (Lickliter & Gottlieb, 1986b).

A further study examined how altering the timing of this social experience affects ducklings' preference for maternal cues. Lickliter and Gottlieb (1987) allowed 24-hr-old ducklings to follow the familiar mallard hen model for 30 minutes to establish imprinting. In one condition, ducklings were reared with siblings until the imprinting training at 24 hr, but from 24 hr until testing at 48 hr, ducklings were reared in isolation. These birds produced no evidence of any preference for the maternal hen over a species-atypical redhead hen during testing. In the second condition, ducklings were reared with siblings both before and after the imprinting trial. Thus, ducklings experienced social interaction from hatching until testing at 48 hr. These ducklings demonstrated a preference for the familiar mallard hen over the unfamiliar redhead hen, providing evidence that social interaction with siblings both before and after imprinting is necessary for subsequent preference of species-typical maternal cues. In sum, the results of these experiments further support the critical role that social interaction with siblings provides in directing species-typical responsiveness to maternal cues (Lickliter & Gottlieb, 1987).

From these studies, it has been established that social interaction with broodmates is a critical component in the development of maternal preferences. Lickliter and Gottlieb (1988) went on to examine whether these findings resulted from generalized social stimulation, or whether ducklings needed specific social experience with same-species siblings. Ducklings were reared with either same-age mallard ducklings, same-age domestic chick hatchlings, or muscovy ducklings. Mallard ducklings demonstrated a preference for the mallard hen model only if they had been allowed social interaction with broodmates of their own species, providing further evidence of the complex and specific influence that social experience can have on early perceptual and social development (Lickliter & Gottlieb, 1988).

Taken together, results from this series of studies demonstrate that species-typical social environments can powerfully impact developing organisms. In the most general sense, these studies (Lickliter & Gottlieb, 1985, 1986a, b, 1987, 1988) provide evidence that developing organisms are actively shaped by the normally occurring experiences they encounter during the process of development. In the case of precocial birds, who are typically reared in broods with groups of same-age siblings, ongoing social experience with these siblings seems to exert a particularly powerful influence on developmental outcomes. In most cases, these influences are non-obvious, in that observed behaviors in response to maternal cues (one type of interaction) are often shaped and supported by early experiences with siblings (a different type of interaction). For instance, Gottlieb (1978) demonstrated that in order for ducklings to exhibit a postnatal preference for a species-specific maternal call, they must hear their own embryonic vocalizations or those of their siblings prenatally, a non-obvious factor which plays an important role in promoting reliable, species-typical outcomes.

Along with research examining social influences on imprinting behavior, research concerned with precocial birds' developing sensory systems has also provided evidence that social experience with siblings can influence perceptual development. Research with bobwhite quail (*Colinus virginianus*) has demonstrated that social interaction with siblings can affect responsiveness to both maternal auditory and visual cues in a number of ways. For example, Lickliter (1989) examined the role that normal interaction with conspecifics plays in bobwhite chicks' responsiveness to species-specific maternal auditory cues, expanding on the literature demonstrating that early social experience with broodmates contributes to the development of early perceptual functioning. In this study, bobwhite chicks were reared either socially or in isolation from their broodmates, to determine whether early social experience would affect responsiveness to maternal auditory cues. Specifically, in one test condition, chicks were reared either socially or in relative isolation, then asked to choose between a maternal bobwhite call or a group of four live siblings at 24 hr and 48 hr after hatching. Chicks reared in isolation preferred the bobwhite maternal call over the group of siblings at both 24 and 48 hr following hatching, while socially reared chicks did not prefer either the maternal call or the group of live siblings. In a second test condition, chicks were reared socially, then were asked to choose between a live bobwhite hen paired with a maternal bobwhite call versus a group of four live siblings at 24 hr and 48 hr after hatching. In contrast with the first testing condition, socially reared chicks did not prefer either the maternal call paired with the live hen over the group of live siblings. Chicks in a third test condition were reared in partial isolation from their siblings; they could see and hear their broodmates but were denied physical contact with them. Chicks in this condition preferred the maternal call at both 24 and 48 hr following hatching. In sum, the results of these experiments provide further evidence for the influence that social experience with siblings can make on subsequent perceptual preferences (Lickliter, 1989). Additionally, this study provides preliminary evidence that one important aspect of social experience involves direct physical contact with broodmates, a non-obvious, experiential contribution to perceptual development.

In a subsequent study, Lickliter and Virkar (1989) found that at one and two days of age, unmanipulated bobwhite quail chicks depend on the auditory component of maternal stimulation. However, by three days of age, quail chicks require combined auditory and visual stimulation to direct their preferences. Furthermore, three-day-old chicks fail to demonstrate a preference for either silent hen models or maternal auditory cues presented alone, but require maternal auditory and visual cues to be paired with each other (Lickliter & Virkar, 1989). These results provided evidence that auditory cues are dominant over visual cues in the period following hatching, which suggests that a functional hierarchy of sensory systems exists in developing bobwhite quail chicks (Lickliter & Virkar, 1989; Lickliter, 1994). It is important to note that these unmanipulated chicks were reared with their siblings from hatching until testing, which provided them with specific auditory, visual, and tactile experiences. In light of previous research examining social experiences with both ducklings and bobwhite chicks (Lickliter, 1989, 1991; Lickliter & Gottlieb, 1985; 1986a, b; 1987, 1988), these results suggest that ongoing social experience with bobwhite siblings may somehow influence these species-typical patterns of responsiveness to maternal auditory and visual cues.

Lickliter, Dyer, and McBride (1993) suggest that perceptual preferences underlying perceptual functioning, which researchers have previously thought to be "innate," are in fact sensitive to a variety of social factors which are present in the young birds' posthatching environment. In reviewing recent work with precocial avian hatchlings, they found that young hatchlings who are denied direct social experience with their siblings consistently demonstrate different auditory and visual perceptual preferences than hatchlings who are allowed ongoing experience with their broodmates during the posthatching period of development. They argue that in order to more fully understand an organism's emerging patterns of behavior, research must include the social environment in which the developing organism is typically embedded and with which it interacts during the course of ontogeny.

In this light, McBride and Lickliter (1993) examined the role of altered social experience on species-typical patterns of perceptual responsiveness by manipulating chicks' early experience with siblings. Chicks in this study were reared postnatally either in a group, in isolation, in partial isolation, or with heterospecific scaled quail chicks. Results revealed that only chicks group-reared with conspecific (bobwhite) siblings and allowed ongoing social, tactile, and visual interaction with these siblings demonstrated normal patterns of sensory development. These findings also provide evidence that the social experiences provided during early development can serve to maintain and facilitate the perceptual and social adaptations that young chicks require early in their development (McBride & Lickliter, 1993).

In addition to maintaining and facilitating behavioral responses, Gottlieb (1991a, 1993) has recently demonstrated the powerful effect that social experiences can have in altering species-typicality, by inducing new patterns of behavior that otherwise would not occur. For example, Gottlieb (1991a) reared mallard ducklings either in isolation or with siblings, and exposed the developing embryos and hatchlings in both groups to an atypical chicken maternal call. Ducklings were then tested to determine their preference between the species-typical mallard hen call or the chicken call they had heard pre- and postnatally. Ducklings reared with siblings demonstrated a preference for the species-atypical chicken call, while isolate-reared ducklings preferred the species-typical mallard hen call. In a subsequent study, Gottlieb (1993) showed that tactile contact with siblings provides a mechanism through which induction of species-atypical behavior takes place.

In light of these past studies, it seems apparent that the social experiences provided to developing organisms can effectively help shape their early perceptual functioning. Additionally, these studies also present a second, less obvious result, namely, that a developing organism's sensory stimulation history provides a particularly useful means to explore the details of how early experience impacts subsequent development. Perceptual inputs can be manipulated at various stages of development, and the effects of modified perceptual experience can be easily tested, especially with precocial organisms. Importantly, the sensory systems of birds and mammals do not become functional at the same time in development. Rather, the onset of functioning of the different sensory systems follows an invariant, sequential pattern (tactile--> vestibular--> olfactory--> auditory--> and visual, Gottlieb, 1971). Because the onset of sensory functioning follows a specific and invariant pattern, this provides a potentially powerful way to examine how alterations in this pattern affect subsequent perceptual responsiveness. Most studies within this area of research have addressed this issue by either adding or taking away sensory stimulation at specific times in either prenatal or postnatal development (Banker & Lickliter, 1993; Lickliter, 1990a, 1994; Lickliter & Lewkowicz, 1995; Lickliter & Stoumbos, 1991, 1992; Sleigh & Lickliter, 1995, in press a, b; Symons & Tees, 1990; Turkewitz & Mellon, 1989). What this work has tended to overlook or undercharacterize is the influence of social experience on early perceptual development.

Developing human and animal infants are, of course, embedded within a rich social network of conspecifics, which provide ongoing sensory stimulation to the developing organism. Within this network, the particular types and amounts of sensory stimulation provided by the organism's immediate social environment may effectively shape the developing organism's perceptual functioning both during prenatal development (Lickliter, 1990a, b; Sleigh, Columbus, & Lickliter, in press; Sleigh &

Lickliter, in press, a) and during postnatal periods (Lickliter, 1989; McBride & Lickliter, 1993, 1994). For example, studies in this line of research have reliably demonstrated that organisms who are reared in isolation from their normal social environment show altered patterns of perceptual functioning. These results suggest that ongoing species-typical sensory stimulation provided by the organism's social interaction with conspecifics helps direct and shape the emergence of perceptual preferences throughout early development.

While developing organisms continuously experience different types and amounts of ongoing sensory stimulation throughout ontogeny, <u>when</u> these specific experiences are encountered during development also affects perinatal perceptual organization. In an early study, Hymovitch (1952) examined how early experience with either enriched environment or deprivation conditions affects perceptual learning ability in rats. Specifically, he found that rats who experienced enriched environment conditions early in life (i.e., rats were reared in a large cage with alleys, runways, apertures, small enclosed areas, etc.), then experienced deprived perceptual experience (i.e., rats were reared in small, stovepipe cages with only airholes, water, and food), demonstrated superior performance in a perceptual learning task when compared to a control group reared in normal mesh cages. However, rats who were reared in the stovepipe cage early in life, and then transferred to the enriched cage condition failed to show this same level of performance, and scored similarly to rats who had never experienced enriched environments. The results of this study suggest that the timing of experience is indeed important in maintaining normal perceptual functioning.

In light of these studies, Turkewitz and Devenny (1993) have proposed that examining the timing of when a particular sensory experience is normally available to the organism may clarify how specific sensory systems interact with each other and how perceptual hierarchies organize and reorganize throughout the developmental process. The sensory systems become functional at different times during ontogeny, and the timing of onset in sensory system functioning provides a species-typical structure to developing sensory systems. Altering the asynchronous onset of function of the sensory systems should result in a change in the nature of early intersensory relationships (Lickliter, 1993).

In addition to the timing of sensory system onset, the timing of sensory experience within these developing systems can affect intersensory development. Specifically, organisms' perceptual functioning can be delayed or facilitated by the type and amount of sensory stimulation organisms experience at different points in time. Lickliter (1993) has suggested that the timing of developmental events also imposes constraints as well as opportunities for the developing organism, and that when an experience occurs in development can be as fundamental to developmental outcomes as what is experienced.

In this light, what specific factors present in the social environment are necessary for organisms to successfully integrate the multitude of perceptual information received from their visual, auditory, vestibular, and tactile sensory systems? Recent studies (Knudsen, 1985; Knudsen & Knudsen, 1985; Lewkowicz & Lickliter, 1994; Stein & Meredith, 1993; Stein, Meredith, & Wallace, 1994) using animal models have provided evidence that experience with integrated auditory and visual information plays an important role in the development of intersensory perception. The social milieu surrounding the developing organism provides one important source for this species-specific integrated auditory, visual, and tactile information. For example, newly born or hatched animals are, in most cases, reared with similar-aged siblings during their early development. This rearing experience provides each developing organism with an interactive opportunity to observe, touch, and hear siblings immediately following birth or hatching, thereby providing them with ongoing integrated multi-sensory information. In other words, when an organism hears a sibling peep or squeak, the organism can also see the sibling vocalizing. When the organism touches a sibling, it also sees and feels the sibling move. The cumulative effect of these ongoing experiences may serve to facilitate intersensory functioning early in development.

Previous studies with bobwhite quail chicks have described the development of intersensory perception by outlining the species-typical pattern of bobwhite chicks' responsiveness to various aspects of maternal auditory and visual cues (e.g., Lickliter, 1993, 1994; Lickliter & Banker, 1994; Lickliter & Virkar, 1989). These studies have shown that newly hatched chicks initially rely on maternal auditory vocalizations to direct their early filial responsiveness, but by several days following hatching, chicks require combined auditory and visual cues to direct their social preferences. Importantly, these species-typical effects were observed in chicks who were reared in normal broods of same-aged, same-species siblings. Chicks who are reared in relative isolation during the postnatal period fail to integrate maternal auditory and visual cues at ages when unmanipulated chicks reliably demonstrate this behavior (McBride & Lickliter, 1993). Specific features of chicks' social interaction thus appear to be important for meditating the normally observed patterns of intersensory responsiveness at different developmental ages.

Lickliter, Lewkowicz, and Columbus (1996) recently examined how alterations in spatial and temporal features of bobwhite chicks' social experience affect chicks' species-typical development of intersensory perception. Chicks were reared with either siblings, siblings and spatially "disembodied" hatchling vocalizations, or siblings in an extreme light-attenuated environment. Results revealed that unmanipulated chicks exhibit a significant preference for integrated maternal auditory and visual stimuli by 72 hr of age, even when these stimuli are species-atypical. In the testing situation, chicks were provided a choice between a silent bobwhite hen model spatially separated from a bobwhite maternal call, or a spatially co-located scaled hen model paired with the bobwhite maternal call. Unmanipulated chicks preferred the species-atypical, co-located stimuli over the spatially separated, species-typical stimuli. In contrast, chicks denied spatially integrated auditory or visual experience with siblings in the days following hatching did not demonstrate this preference for co-located stimuli. Taken together, these results highlight the important role that social experience can play in the emergence of intersensory integration of spatially disparate and co-located stimuli, and further suggest that specific features of this early social experience may mediate chicks' subsequent tolerance for spatial discrepancy in maternal audio-visual cues (Lickliter et al, 1996).

What remains to be explored is what specific features of these social sensory cues affect intersensory development.

The present study provides a further step in unpacking how specific features present in the early social environment serve to impact the development of intersensory integration. Specifically, aspects of the postnatal social environment of a precocial avian species, the bobwhite quail, were manipulated to explore which features of early social experience may affect behavioral responsiveness to integrated maternal auditory and visual cues. Based on previous research examining the role of social experience on development, it seemed likely that the ongoing exposure to siblings in the period following hatching would foster intersensory abilities. In this study, the species-typical social environment of bobwhite hatchlings was altered by providing them with both normal and altered social sensory stimulation at different times in their postnatal development. Their subsequent pattern of responsiveness to integrated maternal auditory and visual cues was then assessed. These manipulations altered the normal relationship between species-specific auditory, visual, and tactile cues normally present in the chicks' postnatal environment, in an attempt to unpack how the timing of presentation of normal social experience affects development of subsequent intersensory perceptual responsiveness.

The proposed experiments attempted to answer the following question: Is the cumulative effect of early experience with continuously available, integrated social cues more effective in facilitating the intersensory integration of maternal cues than social experience occurring later in the posthatch period?

Hypotheses and Predictions

Previous research demonstrates that bobwhite chicks who do not experience typical patterns of interaction with siblings in the early postnatal period fail to demonstrate species-typical patterns of perceptual functioning (McBride & Lickliter, 1993, 1994). These findings suggest that certain aspects of experience with siblings facilitate normal perceptual outcomes. Experience with siblings is characterized by continuously available integrated auditory, visual, and tactile cues, and it seems likely that this accumulation of experience with integrated information may be necessary for subsequent development of intersensory perception. I hypothesized that altering the relationship between auditory, visual and tactile cues provided by siblings in the early postnatal days would result in a delayed preference for integrated maternal audio-visual cues.

Previous research has also demonstrated that the specific timing of the introduction of altered sensory information influences perceptual functioning in developing organisms (Lickliter, 1993; Turkewitz & Devenny, 1993). In particular, several studies from this lab have examined the malleability of early intersensory functioning (Banker & Lickliter, 1993; Lickliter, 1990a, b, 1994; McBride & Lickliter, 1995) by altering the stimulation histories of the different sensory modalities. For example, Lickliter (1990a, b) provided quail chick embryos with unusually early visual stimulation, which resulted in accelerated patterns of postnatal intersensory functioning. In a related study, Banker and Lickliter (1993) manipulated the timing of visual stimulation in bobwhite quail chicks, by providing them either early or delayed visual experience. Chicks receiving delayed postnatal visual experience demonstrated decelerated patterns of intersensory functioning, while chicks receiving prenatal visual experience and delayed postnatal visual experience demonstrated normal patterns of intersensory functioning (Banker & Lickliter, 1993).

These studies demonstrate that early perceptual functioning can be easily altered by specific sensory experience, depending on when these experiences are encountered. Immediately upon hatching, bobwhite chicks are normally presented with an array of visual information, which previously was not available within the *in ovo* prenatal environment. It seems likely that the rapidly developing hatchling's early sensory experience may be more critical in the development of intersensory integration than later postnatal sensory experience. That is, early exposure to integrated social information may buffer the developing hatchling from altered sensory information later in the posthatch environment. In this light, I hypothesized that chicks who received altered sensory information throughout the first 72 hr of postnatal development would demonstrate delayed maternal auditory-visual responsiveness. I also hypothesized that experimental chicks who received normal social experience initially in postnatal rearing, and then subsequently received altered sensory information would respond similarly to unmanipulated control chicks in their responsiveness to maternal auditory-visual cues. In contrast, I hypothesized that chicks who received altered sensory information initially in postnatal development, and then subsequently received unaltered species-typical sensory experience would demonstrate delayed maternal auditory-visual responsiveness. In sum, this study attempted to highlight the role of social experience in facilitating perceptual functioning, and to provide evidence that the timing of specific sensory experience during the early postnatal period is important for facilitation of species-typical perceptual development.

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 292 incubator-reared bobwhite quail chicks (*Colinus virginianus*). Fertile, unincubated eggs were received weekly from a commercial supplier and set in a Petersime Model I incubator, maintained at 37.5°C and 85-90% relative humidity. After 20 days of incubation, eggs were transferred to a hatching tray located in the bottom of the incubator. To control for possible effects of variations in developmental age, only those birds that hatched between the last half of Day 22 and the first half of Day 23 of incubation were used as subjects. 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 two or more different batches (weeks) of eggs. As a result of their incubator rearing, the only sounds to which the hatchlings were exposed to prior to the time of experimental manipulation or the time of 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. Following hatching, subjects in most experimental groups were group-reared in large plastic tubs containing 10 to 14 same-aged chicks to mimic naturally occurring brood conditions (Stokes, 1967). The sound-attenuated room in which the hatchlings were reared is illuminated by a 100-W brooder lamp suspended above the plastic rearing tubs, which maintains an ambient air temperature of approximately 30°C. Food and water were continuously available throughout the duration of each experiment.

Testing

Testing was conducted after hatching at 72 hr (+/- 3 hr) of age. Each chick was tested once in a 5 min simultaneous choice test in a large circular arena, 160 cm in diameter, surrounded by a wall 24 cm in height and draped by an opaque black curtain which shielded 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 10% of the total area of the arena. A midrange dome-radiator speaker is positioned behind the curtain in each of these two approach areas, equidistant from the point at which each subject is placed in the apparatus. Each speaker is hidden by the curtain and 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 opposing 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 particular auditory and visual stimuli presented were alternated between chicks to prevent any possible side bias from influencing results. Each chick was tested only once, and latency of response 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. When, over the course of the 5 min trial, if a chick stayed in one approach area for more than twice the time it spent in the opposing approach area, a preference for that stimulus array was recorded. Occasionally a bird entered the approach areas during a test without showing a preference for either one. This behavior was scored as "No Preference" in the tables showing test results. The subject had to remain in an approach area for at least 10 cumulative seconds for a score to be counted; this criterion prevented any random movements from being counted as a response to the presented stimuli. If a subject did not enter either approach area or if a subject did not accumulate a duration score of 10 cumulative seconds over the course of the trial, it was considered a non-responder and received a score of 300 seconds for latency (the length of the trial) and 0 seconds for duration for both test stimuli.

Subjects in the observational conditions were observed during 10-minute intervals at both 24 and 48 hrs of age, in a procedure similar to that used by McBride and Lickliter (1993). Data were recorded on checklists (see Appendix A) that included (a) whether the subject's eyes were open or closed, (b) whether the subject was alone or in physical proximity (within 1 body length) to 2 or more hatchlings, (c) whether the subject was in direct physical contact with at least 1 other hatchling, (d) whether or not the subject was in behavioral synchrony (engaged in the same behavior) with the majority of the other hatchlings in the brood, (e) whether or not the subject was walking or moving, (f) whether the subject was standing, sitting, or lying, (g) whether the subject was pecking at feed or drinking water, (h) whether the hatchling was silent, or emitting distress or contentment vocalizations, and (i) whether or not the subject was engaged in wing fluttering behavior. Following the final observation period, each subject was also measured on its righting response. This measure has traditionally been used as a measure of animals' overall strength and motor coordination during early postnatal development (McBride & Lickliter, 1993; Pellis, Pellis, & Teitelbaum, 1991). To measure a subject's righting response, each chick was placed on its back on a flat surface, and the time (in seconds) that it took for the subject to turn back over into an upright position was scored.

Data Analysis

The primary data of interest in each experiment were the measures of preference (derived from latency and duration of response) for the auditory and visual stimuli presented during the trial. Three such measures of preference were utilized (1) differences in the latency and (2) differences in the duration of time spent in proximity to each stimulus array by a subject was evaluated by the Wilcoxon matched-pairs, signed-ranks test, and (3) an individual preference, assigned to any subject that stayed in one approach area for more than twice as long as the other, was evaluated by the chi-square test. Significance levels of $p<.05$ were used to evaluate results and all reported p values are two-tailed.

Observational data from control chicks and chicks reared with freeze-dried siblings were also analyzed and compared using t-tests, to determine the percentage of time that subjects from each group spent engaged in each of the behavioral measures. A between-groups comparison of the mean righting response times was also performed.

Experiment 1: Effects of Typical Postnatal Social Experience on Chicks' Intersensory Responsiveness to Maternal Auditory-Visual Cues

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 a species-atypical maternal call 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). This species-typical pattern of responsiveness does not necessarily depend on postnatal exposure to an adult bobwhite hen, but rather can result from bobwhite hatchlings' ongoing social interaction with siblings in the days following hatching (McBride & Lickliter, 1993). Importantly, postnatal experience with siblings is characterized by the spatial and temporal contiguity of auditory, visual, and tactile cues. McBride and Lickliter (1993) showed that unmanipulated chicks who were normally reared with siblings reliably prefer a bobwhite hen paired with a bobwhite maternal call over a species-atypical scaled hen paired with the same bobwhite maternal call.

The purpose of this initial experiment was to replicate previous studies demonstrating that species-typical experience with integrated multimodal cues provided by siblings influences subsequent responsiveness to maternal audio-visual cues. Specifically, the effects of continuous rearing with normal siblings on chicks' responsiveness to maternal auditory and visual cues were assessed in the days following hatching. If continuous exposure to conspecifics' integrated auditory, visual, and tactile cues is important to chicks' early patterns of perceptual responsiveness, then unmanipulated chicks should respond similarly to chicks from earlier experiments (Lickliter & Virkar, 1989; McBride & Lickliter, 1993) by preferring integrated species-typical maternal auditory and visual cues over integrated species-atypical maternal auditory and visual cues.

Method

Twenty bobwhite quail chicks, drawn from four separate hatches, served as subjects. Following hatching, chicks were placed in large plastic tubs (25 cm wide x 15 cm high x 45 cm long) that contained 10 - 14 conspecifics (Stokes, 1967). Subjects thus received continuous integrated tactile, auditory and visual cues from their siblings throughout the first 72 hr following hatching. Testing occurred at 72 hr of age in a simultaneous choice task between integrated species-typical and integrated species-atypical maternal auditory and visual cues. Specifically, chicks were placed singly in the testing arena and given a choice between a bobwhite hen paired with a bobwhite maternal call and a species-atypical scaled quail hen (*Calipepla squamata*) paired with the same bobwhite maternal call. Choice, latency, and duration of response were scored as described in the General Methods section.

Results and Discussion

The results of Experiment 1 are shown in Tables 1 and 2. Unmanipulated chicks continuously reared with siblings in a species-typical environment demonstrated a significant preference for the species-specific bobwhite hen paired with the bobwhite maternal call at 72 hrs following hatching, $\chi^2(2) = 12.4$, $p < .01$. 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 paired with the bobwhite call than to the species-atypical scaled hen paired with the bobwhite maternal call, ($z = 3.38$ for latency, $z = 3.14$ for duration, $p < .01$ in both cases).

These findings replicate results found with unmanipulated chicks in several previous studies (Lickliter 1994; Lickliter & Virkar, 1989; McBride & Lickliter, 1993). In these studies, chicks reared with siblings in the absence of maternal cues initially show a naive preference for maternal auditory cues at 24 and 48 hrs following hatching, but require combined maternal auditory and visual cues to direct their social preferences by 72 hrs after hatching. It is important to note that from hatching until testing, hatchlings are reared normally with conspecific siblings, and this experience with siblings is characterized by integrated tactile, auditory, and visual information in both time and space. What remains unclear is how this social experience leads to the emergence of intersensory integration, and whether these species-typical patterns of perceptual preference can be altered by both the <u>type</u> of social experience that is encountered and also the <u>timing</u> of when these social experiences occur. With this in mind, the purpose of the next experiment was to 1) alter the type of social experience chicks to which chicks were exposed, and 2) to investigate the role of either early or later altered tactile experience in chicks' ability to integrate maternal auditory and visual cues by 72 hrs of age.

Experiment 2: Effects of Timing of Postnatal Exposure to Species-Atypical Tactile Cues on Maternal Auditory-Visual Responsiveness

Several studies have demonstrated that physical contact with siblings in the period prior to and following hatching is necessary for the emergence of normal patterns of perceptual development (Lickliter & Lewkowicz, 1995; McBride & Lickliter, 1993; Sleigh, Columbus, & Lickliter, in press). These studies demonstrate that chicks reared in isolation, and thus denied typical physical contact with same-aged siblings, reliably demonstrate delayed patterns of typical perceptual functioning. For example, Lickliter and Lewkowicz (1995) found that chicks incubated in physical isolation from broodmates during the late stages of prenatal development responded to maternal auditory cues into later stages of the postnatal period than communally incubated chicks. Chicks incubated in isolation also failed to learn an individual bobwhite maternal call, a behavior reliably seen in unmanipulated chicks. Additionally, isolation-reared chicks failed to respond to maternal visual cues at ages communally incubated chicks typically display this visual responsiveness (Lickliter & Lewkowicz, 1995). Similarly, Sleigh, Columbus, and Lickliter (in press) also demonstrated that chicks reared in isolation prenatally failed to demonstrate prenatal auditory learning of the bobwhite maternal call. Finally, McBride and Lickliter (1993) demonstrated that hatchlings reared in postnatal isolation from their siblings failed to demonstrate intersensory responsiveness to integrated maternal auditory and visual cues at ages when socially reared hatchlings demonstrate this ability. Taken together, results from these studies suggest that some aspect of physical interaction with siblings is necessary for maintenance of species-typical perceptual development.

In this light, the current experiment examined whether exposure to normal and attenuated sibling tactile cues continuously presented throughout postnatal rearing, or presented either in the first or next half of postnatal rearing, leads to altered intersensory responsiveness to maternal audio-visual cues.

Method

Rearing

Subjects were sixty bobwhite quail chicks, drawn from seven separate hatches. Following hatching, chicks were divided into three groups. The first group (n = 20) was reared in social groups of 5 - 7 living siblings and 5 - 7 freeze-dried siblings for the first 72 hrs of postnatal rearing. These freeze-dried siblings are stationary, and thus provide attenuated tactile stimulation to the developing hatchlings. The freeze-dried bobwhite chick models were prepared using a Labconco Lyph-Lock 6.0 Liter Freeze-Dry system. Freeze drying is the process of removing the moisture from a biological product, while maintaining the product's morphological and chemical structure. While conventional drying procedures damage cells by causing the material to shrink, freeze-drying allows the specimen to remain life-like, by removing only the water within the cell structures. Freeze drying is most often used in situations in which long-term storage stability of biological structures is desired. Therefore, the freeze-dried chicks appear essentially the same as live bobwhite chicks, except for the lack of normally present movement and vocalizations exhibited by living chicks. Thus, chicks in this experiment received the atypical experience of attenuated tactile experience from hatching until testing at 72 hrs of age.

The second group of chicks (n = 20) was reared in social groups of 5 - 7 living siblings and 5 - 7 freeze-dried siblings for the first 36 hrs following hatching. Thus, these chicks received the atypical experience of attenuated tactile experience for the first 36 hrs following hatching. From 36 hrs until testing at 72 hrs, the chicks were reared in groups of 10 - 14 live same-aged siblings. The third group (n = 20) was reared in normal groups of 10 - 14 living siblings for the first 36 hrs following hatching. From 36 hrs until testing at 72 hrs, chicks were reared with 5 - 7 living siblings and 5 - 7 freeze-dried siblings. Food and water was continuously available to the subjects throughout the duration of the experiment.

Testing

Chicks from the all three experimental groups were individually tested at 72 hr following hatching in a simultaneous-choice test between a stuffed bobwhite hen paired with a bobwhite maternal call and a scaled hen paired with the same bobwhite maternal call. Thus chicks were able to respond to either the bobwhite hen co-located with the bobwhite call or the scaled hen co-located with the bobwhite call. During testing, all calls were broadcast at a uniform peak intensity of 65 dB. Choice, latency, and duration of response were scored as described in the General Methods section.

Results and Discussion

The results of Experiment 2 are shown in Tables 3 and 4. Chicks reared with both normal and lyophilized (freeze-dried) siblings from hatching until testing at 72 hrs failed to demonstrate a significant preference for either hen model paired with the bobwhite maternal call, $\chi^2(2) = 1.1$, $p > .05$. Additionally, subjects reared with freeze dried siblings during either the first 36 hrs or second 36 hrs following hatching also failed to demonstrate a significant preference for either hen model, (first 36-hr group, $\chi^2(2) = 2.55$, $p < .05$; second 36-hr group, $\chi^2(2) = 0.75$, $p > .05$). Analysis of latency and duration scores supported these results. There were no significant differences in chicks' latency or duration scores to either hen model paired with the bobwhite call at 72 hrs of age for the 72-hr experience group ($z = 0.57$ for latency, $z = 0.5$ for duration, $p > .05$ in both cases), for the first 36-hr experience group ($z = 0.22$ for latency, $z = 0.48$ for duration, $p > .05$ in both cases), or for the second 36-hr group ($z = 0.58$ for latency, $z = 0.83$ for duration, $p > .05$ in all cases).

These findings stand in contrast to results obtained from unmanipulated chicks in Experiment 1, in which chicks significantly preferred species-typical audio-visual maternal cues by 72 hrs following hatching. In the present experiment, chicks reared with attenuated tactile sensory stimulation for the first 72 hrs following hatching or during early or later postnatal development failed to demonstrate a significant preference for species-typical maternal auditory and visual cues. These results suggest that altered tactile experience leads to interference with chicks' intersensory development, regardless of when the altered tactile experience occurs, and further supports previous evidence that tactile sensory stimulation plays a particularly powerful role in influencing species-typical perceptual development. In particular, it appears that altered tactile experience presented at any time during postnatal development is sufficient to disrupt normal perceptual development, even when chicks' experience normal tactile stimulation either before or after being exposed to altered tactile sensory cues. Therefore, in this particular sensory modality, it appears that the timing of presentation of this altered experience is not as influential as the <u>type</u> of altered sensory information experienced.

Observational Data: Effects of Normal and Altered Tactile Experience on Several Behavioral States in Bobwhite Quail

Previous studies with bobwhite quail chicks have demonstrated that socially reared bobwhite quail chicks huddle together with their siblings during a majority of their early development (McBride & Lickliter, 1993). During early postnatal development, bobwhite quail chicks are unable to thermoregulate, an ability that emerges at three to four weeks of age (Stokes, 1967). This raises the interesting possibility that tactile contact with siblings may serve, in part, as a source of heat for the developing hatchlings. In this light, the perceptual delays shown by chicks in Experiment 2 might have resulted from these chicks' experiencing decreased body temperature, since they were reared with only 5 - 7 live siblings, as opposed to the normal brood size of 10 - 14 live chicks. This experience in and of itself might have led to the chicks' observed delays in perceptual functioning. To investigate this possibility, chicks reared in normal groups of 10 - 14 siblings, and chicks reared with attenuated tactile sensory stimulation were observed at two points during their early postnatal development on a variety of behavioral measures.

The observational data is summarized in Tables 5 and 6. At 24 hrs of age, control chicks demonstrated significantly more drinking behavior, $t(42) = 2.94$, $p < .01$, and significantly less wing fluttering behavior, $t(42) = 2.82$, $p < .01$, than chicks reared with altered tactile experience. By 48 hrs of age, however, there were several additional differences observed between the two groups. Specifically, control chicks spent significantly less time awake than experimental chicks, $t(41) = 2.07$, $p < .05$. Control chicks also demonstrated significantly less time standing, $t(41) = 4.71$, $p < .001$, and engaging in wing fluttering behavior, $t(41) = 2.07$, $p < .05$, than experimental chicks, and engaged in significantly more lying, $t(41) = 2.04$, $p < .05$, and sitting postures, $t(41) = 3.78$, $p < .001$, than experimental chicks.

While these differences between groups are interesting, they do not provide enough evidence that the two rearing conditions differ because of different amounts of thermoregulation provided by siblings. Specifically, chicks in both groups spent the majority of the observation time in physical proximity or direct contact with at least 2 other hatchlings. In other words, chicks in both groups spent most of the time huddled together with their broodmates at both 24 hrs, $t(42) = 1.15$, $p > .05$, and 48 hrs, $t(42) = 1.63$, $p > .05$, following hatching. These results suggest that chicks in both conditions were receiving equal or similar amounts of tactile stimulation and thermoregulation from their siblings. When the subjects in both conditions were moving, they were doing so in synchrony with each other and as a group, and there were no significant differences between the groups in these particular behaviors at either 24 hrs, $t(42) = 0.19$, $p > .05$, or 48 hrs, $t(41) = 1.75$, $p > .05$, following hatching. Additionally, chicks in both rearing conditions spent less than 10% of the observation time emitting contentment, $t(42) = 1.41$, $p > .05$, or distress vocalizations, $t(42) = 1.11$, $p > .05$, or eating, $t(42) = 0.51$, $p > .05$, and there were no significant differences between the groups at any age observed. Finally, the mean righting response times of chicks in both conditions were also not significantly different at 48 hrs post-hatching, $t(41) = 0.24$, $p > .05$. These results suggest that the delayed audio-visual responsiveness in chicks reared with freeze-dried siblings is most likely not due to decreased sensorimotor coordination in these chicks.

In sum, these findings suggest that the overall amount of stimulation is not substantially attenuated within the groups reared with freeze-dried siblings. Rather, it seems that there is a qualitative difference between the two rearing conditions, and that this difference may result in the observed patterns of perceptual responsiveness.

In the present experiment, no differences in sensory responsiveness were found in the timing of postnatal presentation of altered tactile stimulation. However, it is possible that since the tactile system becomes functional during prenatal development, hatchlings' tactile systems are more disrupted by substantial postnatal alterations to information from this modality. The purpose of the next experiment was to see if the findings from this experiment generalize to a different type of sensory information within a separate sensory modality. Specifically, I assessed whether the timing of experience with altered auditory sensory cues influences perceptual responsiveness.

Experiment 3: Effects of Timing of Postnatal Exposure to Species-Atypical Auditory Cues on Maternal Auditory-Visual Responsiveness

Although previous experiments have demonstrated that postnatal experience with conspecifics results in species-typical patterns of perceptual responsiveness (McBride & Lickliter, 1993), little research has focused on how spatial and temporal features of this experience with social sensory cues influences intersensory development. Recently, however, Lickliter, Lewkowicz, and Columbus (1996) demonstrated that altering chicks' early postnatal auditory experience modified their emerging preference for auditory-visual spatial congruity. Specifically, chicks who were exposed to augmented, spatially disparate hatchling contentment calls from hatching until testing at 72 hrs failed to demonstrate a preference for integrated maternal audio-visual cues over spatially disparate maternal audio-visual cues. These results suggest that early postnatal experience with disembodied auditory stimulation can alter chicks' sensitivity to the spatial colocation of sights and sounds.

In this light, the purpose of the present experiment was to investigate how the timing of experience with altered auditory cues in the postnatal period determines subsequent responsiveness to maternal audio-visual cues. Specifically, the effects of providing disembodied auditory cues from hatching until testing at 72 hr on chicks' intersensory responsiveness to maternal auditory-visual cues were examined. Additionally, to determine whether the earlier or later posthatch period is more influential on responsiveness to maternal cues, I examined the effects of providing chicks with disembodied auditory cues during either the first 36 hrs vs. the next 36 hrs of postnatal rearing. If continuous exposure to normal auditory cues is important to chicks' early patterns of perceptual responsiveness, then chicks' receiving altered auditory cues should respond differently than control chicks by failing to demonstrate a preference for integrated, maternal audio-visual cues at 72 hr of age. Additionally, if chicks who receive disembodied auditory cues during the first half of their postnatal experience with siblings respond differently than those chicks who receive these disembodied auditory cues during the latter portion of postnatal rearing, it would suggest that chicks are differentially responsive to integrated sensory cues presented during different periods of their postnatal development.

Method

Rearing

Sixty bobwhite quail chicks, drawn from seven separate hatches, served as subjects. Following hatching, the chicks were separated into three groups. The first group of chicks (n = 20) was reared with normal live siblings and disembodied chick contentment calls four times a day (total = 180 min per day) from hatching until testing at 72 hrs. Thus, the chicks received a total of 540 min of altered auditory stimulation throughout the first 72 hrs of postnatal rearing.

The contentment call recordings used in this experiment were obtained from observations of socially reared bobwhite hatchlings in a previous study (McBride & Lickliter, 1994). The prepared tape loops were played on two Marantz model PMD 221 portable cassette recorders located 80 cm above the chicks' rearing tubs. The tape loops were played concurrently and the recorded calls were played at a uniform peak intensity of 65 dB, as measured by a Bruel & Kjäer Model 2232 sound level meter.

The second group of chicks (n = 20) was reared with normal siblings until 36 hours of age. From 36 hours of age until testing at 72 hrs, these chicks were reared with siblings and, in addition, received 45 min of recorded disembodied chick contentment calls every six hours throughout the last 36 hrs until testing. Thus, the chicks received normal auditory stimulation from siblings during the first 36 hrs, then received a total of 270 min of atypical auditory stimulation for the last 36 hrs of their posthatch rearing. This manipulation effectively provided discontinuous exposure to integrated auditory information. Food and water was continuously available to the chicks throughout the experiment.

To determine whether differences in intersensory development occur between the early or later posthatch periods, chicks in the third group (n = 20) were reared with normal siblings and 45 min every 6 hrs (total = 270 min) of spatially disparate chick contentment vocalizations until 36 hrs of age. From 36 hours of age until testing at 72 hrs, these chicks were reared with normal siblings. Thus, the rearing conditions for this group were reversed from those in the second group of this experiment.

Testing

Testing occurred at 72 hrs of age, in the procedure described in the previous experiment. Chicks from all three groups were tested in a simultaneous choice task between a stuffed model of a species-typical bobwhite hen presented with a bobwhite maternal call, versus a stuffed model of a species-atypical scaled hen paired with the same bobwhite maternal call. Thus, chicks could choose between a colocated bobwhite hen and call, and a colocated scaled hen and bobwhite call. Choice, latency, and duration of response were scored as described in the General Methods section.

Results and Discussion

The results of this experiment are shown in Tables 7 and 8. As can be seen in the tables, chicks reared with 72 hrs of disembodied auditory stimulation failed to demonstrate a significant preference for either the bobwhite hen or scaled hen model, $\chi^2(2) = 2.02$, $p > .05$. Chicks reared with disembodied contentment vocalizations during either the first 36 hrs or second 36 hrs following hatching also failed to demonstrate a preference for either hen model, (first 36-hr group, $\chi^2(2) = 5.20$, $p > .05$; second 36-hr group, $\chi^2(2) = 2.02$, $p > .05$), regardless of when the altered auditory stimulation was presented. Analysis of latency and duration scores further supported these results, with chicks showing no differences in latencies or durations for either hen model at 72 hrs of age in the 72-hr experience group ($z = 0.11$ for latency, $z = 0.07$ for duration; $p > .05$ in both cases), in the first 36-hr experience group ($z = 0.07$ for latency, $z = 0.02$ for duration; $p > .05$ in both cases), or in the second 36-hr group ($z = 0.49$ for latency, $z = 0.30$ for duration; $p > .05$ in both cases).

These results stand in contrast to unmanipulated chicks in Experiment 1, in which chicks significantly preferred species-specific maternal auditory-visual cues by 72 hrs of age. These results suggest that normal auditory experience is necessary for maintaining species-typical perceptual development. More specifically, since hatchlings who experience altered auditory stimulation at any point in postnatal development failed to demonstrate normal perceptual responsiveness, these findings suggest that altering normal auditory stimulation can substantially disrupt species-typical intersensory development. Interestingly, the current findings parallel those found in Experiment 2, in which chicks who received altered tactile experience also showed delayed intersensory responsiveness, regardless of whether the altered stimulation was presented early or later in postnatal development.

Based on these findings, it appears that like the tactile system, the chick's auditory system is also highly susceptible to alterations in normal auditory experience, whenever these experiences may occur during postnatal development. Since the auditory system also becomes functional during prenatal development, it seems likely that postnatal disruptions to normal auditory experience may provide powerful reorganizing influences on chicks' perceptual functioning.

In this light, the next experiment was designed to examine how altered visual stimulation during postnatal development may influence chicks' perceptual functioning. The visual system does not become functional until the postnatal period of development, and is thus a later developing sensory system than the tactile and auditory sensory modalities (see Gottlieb, 1971). Therefore, the visual system may be more susceptible to alterations in the timing of abnormal visual sensory input, since it is becoming functional during the postnatal period. The following experiment was designed to examine this possibility.

Experiment 4A: Effects of Timing of Postnatal Exposure to Species-Atypical Visual Cues on Maternal Auditory-Visual Responsiveness

Previous studies have demonstrated that visual experience during the postnatal environment is important to the development of intersensory responsiveness (Banker & Lickliter, 1993; Lickliter, Lewkowicz, & Columbus, 1996). Specifically, Banker and Lickliter (1993) found that chicks who were denied postnatal visual experience (by means of eye patches) failed to demonstrate a preference for integrated maternal auditory and visual cues into later stages of development than control chicks.

Additionally, Lickliter, Lewkowicz, and Columbus (1996) found that chicks who were reared in postnatal conditions of extreme light-attenuation from hatching until testing at 72 hr also failed to demonstrate normal patterns of intersensory development. That is, chicks who were denied integrated visual information from siblings failed to respond to integrated maternal auditory and visual cues at 72 and 96 hrs of age, a response reliably seen in unmanipulated chicks.

Since chicks' visual systems develop primarily during the post-hatch period, it seems likely that this system is highly susceptible to the type of sensory manipulations experienced during the postnatal period. Additionally, early in development, each sensory system is influenced by the current sensory experience, as well as the sensory history of the organism. In this light, the current experiment examined the effects of providing altered visual cues to bobwhite hatchlings at either early or later times during postnatal development.

Methods

Rearing

Sixty bobwhite quail chicks, drawn from nine separate hatches, served as subjects. Following hatching, chicks were reared in one of three groups. To determine the effects of altered visual stimulation on intersensory responsiveness, the first group (n = 20) was reared in a darkened portable brooder for the first 72 hrs of postnatal age (from hatching until testing). Chicks in this condition were removed from the brooder and allowed to adjust their eyes to the light of the testing room for a period of 2 minutes prior to testing.

The brooder was placed in a darkened room and covered with black paper and black fabric to eliminate the opportunity for postnatal experience with patterned light and with the visual features of their siblings. While we can not be sure that this manipulation eliminated all visual experience for each subject, the dark rearing condition drastically attenuated normal visual experience for the hatchlings. Chicks were able, however, to physically contact and hear their siblings present in the brooder. Food and water was continuously available to the chicks throughout the experiment.

The second group (n = 20) was reared in the darkened portable brooder for the first 36 hrs following hatching, which provided altered visual information, in that chicks were able to hear and touch, but not see, siblings. From 36 hrs until testing at 72 hrs, chicks in the first group were transferred to a sound-attenuated rearing room and reared in normal, lighted conditions with siblings, providing them with typical visual and social experience. The third group (n = 20) was reared in normal, lighted conditions with a group of same-aged siblings for the first 36 hrs post-hatching, providing them with normal, integrated visual information. From 36 hrs until testing at 72 hrs, the chicks were transferred to the dark-rearing brooder and reared in light-attenuated conditions with siblings. Chicks who were dark-reared in the latter half of postnatal rearing (from 36 hrs to testing at 72 hrs) were removed from the brooder and allowed to adjust their eyes to the light of the testing room for a period of 2 minutes prior to testing.

Testing

All subjects were individually tested at 72 hr following hatching. Chicks from all three groups were tested in a simultaneous choice task between a stuffed model of a bobwhite hen paired with a bobwhite maternal call and a species-atypical scaled hen paired with the same bobwhite maternal call. Thus, chicks were asked to choose between a bobwhite hen paired with the bobwhite maternal call, and a species-atypical scaled hen and the same bobwhite call. This test determined how chicks responded to species-specific maternal auditory and visual cues. Choice, latency, and duration of response were scored as described in the General Methods section.

Results and Discussion

Results of this experiment can be seen in Tables 9 and 10. Chicks who were reared in darkened conditions throughout the first 72 hrs following hatching failed to demonstrate a significant preference for either hen model employed in the testing situation, $\chi^2(2) = 4.90$, $p > .05$. Analysis of latency and duration scores supported this result, with chicks showing no significant difference in latencies for either choice ($z = 0.63$, $p > .05$) or durations ($z = 1.21$, $p > .05$). Chicks who were dark-reared during the first 36 hrs following hatching also failed to show a preference for either hen model, $\chi^2(2) = 5.27$, $p > .05$. Analysis of latency and duration scores supported these results: chicks did not differ in their latencies or durations for either auditory-visual choice ($z = 0.41$ for latency, $z = 0.61$ for duration; $p > .05$ in both cases). These results stand in contrast to those found in Experiment 1, in which unmanipulated chicks demonstrated a preference for the bobwhite hen and call at 72 hrs, indicating that chicks in both of these conditions have delayed intersensory responsiveness.

In the third group, however, chicks who were normally reared for the first 36 hrs following hatching, then transferred to darkened conditions displayed a significant preference for the bobwhite hen paired with the bobwhite maternal call versus the scaled hen paired with the same bobwhite maternal call at 72 hrs of age, $\chi^2(2) = 7.35$, $p < .05$. Analysis of latency and duration scores support these findings. Chicks in this condition displayed significantly shorter latencies ($z = 2.29$, $p < .05$) and longer durations ($z = 1.77$, $p < .05$) in their responsiveness to species-specific maternal audio-visual cues. These findings parallel those of unmanipulated chicks in Experiment 1, and suggest that chicks in this group have species-typical patterns of early perceptual development.

Taken together, results from this experiment provide evidence that continuously available integrated visual information is necessary for subsequent species-typical perceptual functioning. These findings also suggest that early disruptions to visual sensory input may interfere with normal intersensory development, while later alterations may be less influential on perceptual functioning. In a more general sense, these findings suggest that the visual system may be differentially susceptible to altered sensory information during the postnatal period. In relation to results from Experiments 2 and 3, it appears that the visual system is more influenced by the timing of sensory stimulation during the postnatal period, while the tactile and auditory sensory systems are less influenced by these manipulations in timing during postnatal development.

Experiment 4B: Effects of Light-Attenuated Rearing Conditions on Chicks' Visual Capacities

It is possible that the results obtained from Experiment 4A might be due to adverse effects of the dark-rearing procedure on bobwhite chicks' eyesight. In other words, the lack of normally available light might have damaged the chicks' ability to see, which would preclude them from being able to choose between the available stimuli during the testing situation. To determine if this procedure did, in fact, damage chicks' eyes, I employed a color discrimination test on both control chicks and chicks who were dark-reared.

Bobwhite quail, like most birds, have excellent color vision. In fact, this ability to discriminate between different wavelengths of light has been used by a number of researchers to investigate the influence of difference experiences with colored objects and foods on developmental preferences (Fischer, Morris, & Ruhsam, 1975; Jones, 1986; Kovach, 1974; Pank, 1976). For example, Mastrota and Mench (1995) found that unmanipulated bobwhite chicks display different levels of responding to various colors by 24 hr of age. Chicks were presented with a display of blue, red, green, and yellow pins at 24 hr of age, and both the number of first pecks and the total number of pecks were calculated to measure preference. Results revealed that bobwhite chicks demonstrate a descending order of preference among the four colors (blue>green>yellow>red) (Mastrota & Mench, 1995).

The present experiment investigated whether dark-reared chicks demonstrate the same pattern of color preference as seen in unmanipulated control chicks. While we could not be certain that color discrimination ability rules out the possibility that other visual capabilities may be damaged (such as the ability to discriminate form), it seemed likely that if chicks could successfully discriminate between wavelengths of light, their vision had not been compromised to the degree to preclude them from discriminating forms and patterns.

Method

Forty quail chicks, drawn from five different hatches, served as subjects. Following hatching, the chicks were separated into two groups. Chicks in the control group (n = 20) were reared in normal, lighted postnatal conditions, with a group of 10-14 same-aged siblings. At 72 hrs of age, these chicks were tested in the sound-attenuated rearing room. Chicks were singly tested in a plastic rearing tub as described in the General Methods section, in a simultaneous choice test between a blue or a red dot. Previous studies (e.g. Mastrota & Mench, 1995) have demonstrated that bobwhite chicks differentially prefer colors in an invariant pattern early in development. Chicks were observed by trained undergraduates, blind to the experimental condition, for a period of 5 minutes from the time the colored dots were presented through the duration of the trial. The dots were simultaneously presented to chicks, and the side presentation of colored dots was counterbalanced across subjects to control for possible side bias.

The number of first pecks and total number of pecks on each colored dot was recorded and tallied, to determine if chicks demonstrate more pecking towards one color than the other.

Chicks in the experimental group (n = 20) were dark-reared from hatching until testing at 72 hrs of age. Chicks were singly placed in a plastic rearing tub, and were simultaneously presented with either a blue dot or a red dot, which were stuck to the side of the rearing tub. The side presentation of these colored dots was counterbalanced across subjects. Chicks were observed in the same procedure employed with control chicks, and their pecking behavior was recorded by trained undergraduates, blind to the experimental condition.

Results and Discussion

Results from this experiment are shown in Table 11. As can be seen in the tables, results from this test were inconclusive, in that all chicks in both conditions failed to respond to either dot during the test trials. Therefore, no conclusions can be made from the color discrimination test about whether or not the dark-reared birds have damaged eyesight.

In light of these results, it was still a concern that the darkened environment had potentially damaged experimental chicks' eyesight. As a second manipulation check, four additional chicks were dark-reared from hatching until 48 hrs following hatching in the normal dark-rearing incubator, then were transferred at 48 hrs to a darkened incubator that contained water, but no food. Thus, these chicks were food-deprived for 24 hrs before testing at 72 hrs of age. At 72 hrs of age, chicks were placed in a plastic rearing tub with a few grains of food in a lighted room and were observed for a 15 minute interval. It was hypothesized that if chicks could still see after 72 hrs of dark-rearing, and they had been food deprived, they would peck at the food provided in the tub.

Only one of the chicks observed pecked at the food, while the other three lay in the corner of the tub. Since three out of four chicks were unable to stand up, these results may indicate that the food-deprivation condition weakened the chicks' ability to peck at food. However, the one chick who could walk did, in fact, peck directly at food, which suggests that it could see the food.

General Discussion

This study examined how both timing of sensory experience and the type of sensory experience influence postnatal perceptual preferences in bobwhite quail. This was accomplished by altering various aspects of chicks' social experience during the first 72 hours of the postnatal period. Specifically, sensory input from the tactile, auditory, and visual modalities was either altered or attenuated in an attempt to assess the role of experience in maintaining or delaying chicks' intersensory responsiveness to maternal auditory and visual cues. Chicks reared in normal social environmental conditions demonstrated a significant preference for the species-specific bobwhite hen model paired with the bobwhite hen maternal call by 72 hrs of age (Experiment 1). These results successfully replicated earlier studies examining the development of intersensory perception in bobwhite quail chicks (Lickliter & Virkar, 1989; McBride & Lickliter, 1993). Chicks reared with altered tactile sensory stimulation for the first 72 hrs follow ing hatching, or during the first or last 36 hrs following hatching failed to respond to species-typical maternal auditory-visual cues at 72 hrs, a response reliably seen in unmanipulated chicks (Experiment 2). By examining observational data from unmanipulated chicks and chicks reared with freeze-dried siblings, the results found in Experiment 2 did not appear to result from decreased amounts of thermoregulatory stimulation available in the altered tactile condition. Rather, there appears to be a qualitative difference between the type of chicks' experience with normal, living siblings, and static, non-moving siblings. Further results revealed that chicks reared with altered auditory sensory stimulation for the first 72 hrs following hatching, or during the first or last 36 hrs following hatching also failed to demonstrate a species-typical preference for the bobwhite hen paired with the bobwhite call at 72 hrs (Experiment 3). Finally, chicks reared with altered visual sensory stimulation during the first 72 hrs or during the first 36 hrs following hatching also demonstrated delayed intersensory functioning. However, chicks receiving altered visual stimulation during the last 36 hrs post-hatching demonstrated a significant, species-typical perceptual preference for the bobwhite hen paired with the bobwhite call at 72 hrs post-hatching, a response reliably seen in control chicks (Experiment 4).

To further support the hypothesis that an interaction between type of stimulation and timing of stimulation exists, a two-way analysis of variance was analyzed. ANOVA results revealed that there was a significant main effect for timing of stimulation in latency scores for the bobwhite hen paired with the bobwhite call, $F(2, 162) = 3.46$, $p < .05$. In other words, chicks demonstrated significant differences in duration scores, depending on when they receive altered sensory stimulation. Post hoc analyses using Tukey's HSD (unequal N's) revealed that chicks who received altered visual stimulation during the second 36 hrs of postnatal development demonstrated significantly shorter latencies than chicks receiving this altered visual stimulation during the first 36 hrs of postnatal development, q(9, 162) = 57.79, $p < .05$. To see if these effects extended to duration scores, a type x timing, two-way analysis of variance was also analyzed using duration scores for the bobwhite hen paired with the bobwhite call. ANOVA results revealed that there was a significant interaction effect between type of stimulation and timing of stimulation, F(4, 162) = 3.23, $p < .01$. In other words, chicks demonstrated significant differences in duration scores for the bobwhite hen paired with the bobwhite call depending on both the type and timing of sensory experience. Post hoc analyses of this interaction using Tukey's HSD (unequal N's) revealed that chicks who received altered visual stimulation for the second 36 hrs demonstrated significantly longer durations at the bobwhite hen paired with the bobwhite call than chicks who received this stimulation for the entire first 72 hrs of postnatal development, q(9, 162) = 135.68, $p < .01$, or chicks who received altered auditory stimulation for the first 36 hrs of development, q(9, 162) = 57.8, $p < .05$. Taken together, these results indicate that both type of stimulation and the timing at which this stimulation occurs work in concert to provide constraints for the developing organism.

The present results support previous research indicating that the sensory systems develop sequentially and are hierarchically organized (Gottlieb, 1971; Turkewitz & Kenny, 1982). Specifically, Turkewitz and Kenny (1982) propose a theory of perceptual development in which constraints inherent in the sequential onset of sensory functioning provide a powerful organizational function on each organism's perceptual development. From this view, limitations within the sensory modalities at differing points in time provide a valuable structure within which each developing sensory system can fully develop with little or no interference from competing sensory systems. In addition to structuring development within a sensory system, these limitations influence the development of relationships between sensory systems (Turkewitz & Kenny, 1982). Furthermore, these relationships are dynamic and changing throughout different times in development, which allows for the eventual development of intersensory perceptual abilities. Finally, the type, amount, and timing of sensory stimulation interact with characteristics of the developing organism to influence subsequent perceptual abilities and preferences (Gottlieb, Tomlinson, & Radell, 1989; Lickliter, 1990b, 1993; Lickliter & Lewkowicz, 1995; Sleigh & Lickliter, 1995; Turkewitz & Kenny, 1982).

Findings from the current study support this model of perceptual development. Specifically, Turkewitz and Kenny (1982) suggest that early stages of development are characterized by competition within a sensory system, but little or no competition between systems (such as the tactile and/or auditory system). During the later stages of perceptual development, the emergence of newly functioning sensory systems (such as the visual system) results in competition between sensory systems, which restructures earlier-developed systems. In summary, this view holds that the emergence of competition between sensory systems at different times during development results in disruption of old patterns of perceptual organization and leads to more advanced reorganization of perceptual function (Turkewitz & Kenny, 1982).

In the present study, bobwhite quail chicks receiving altered tactile and auditory experience (Experiments 2 and 3) during the postnatal period failed to respond to multimodal cues at an age when unmanipulated chicks reliably demonstrate this preference. This absence of responsiveness to maternal auditory-visual cues provides evidence that interference with visual responsiveness occurred as a result of chicks' species-atypical sensory experience. During species-typical development, chicks are normally presented with an array of visual information upon hatching, which they subsequently integrate with both tactile and auditory information by 72 hrs of age (Lickliter & Virkar, 1989; McBride & Lickliter, 1993). Since both the tactile and auditory sensory systems develop prenatally, altering the nature of tactile and auditory stimulation during the postnatal period potentially competes with the postnatally developing visual system and thus delays its species-typical pattern of development. This competition does not typically occur in normal rearing conditions, in which chicks are exposed to species-typical tactile and auditory cues, which allows the visual system and intersensory abilities to develop with little interference from competing modalities. Utilizing this framework would suggest that in Experiments 2 and 3, the distinctions between "early" and "later" posthatch periods could actually both be conceptualized as later periods in the sensory development of these particular sensory modalities, since they become functional during the prenatal period. Therefore, in the present study, the visual system is unique in its sensitivity to experience during the postnatal period, since it normally becomes functional during this time period. However, since the current study used a precocial organism, future studies should examine whether this pattern of sensory development shifts forward to the postnatal period and progresses in the same sequence in altricial infants' sensory development. Additionally, the current study focused on the perinatal and early postnatal period of development of a highly precocial organism. Future studies should examine how early sensory experiences affect later developmental outcomes, by utilizing longitunal methods from infancy until adulthood with a variety of species.

In light of these results supporting the existence of a sensory hierarchy, it is important to mention that the developing sensory systems are linked throughout both prenatal and postnatal periods of development in most species. Because of these linkages, any analysis of developmental timing within a sensory modality must take into account the status of functioning within the various other sensory modalities, as well as the relationship between them. Several lines of research utilizing both altricial and precocial animal models have examined how these relationships between modalities develop at both behavioral and neurological levels of analysis. For instance, Meredith and Stein (1986a, b) have shown that responses of a neuron to stimuli from one modality can be influenced by inputs from other sensory modalities. They examined neurons in the superior colliculus of the cat, which contains a multitude of neurons that respond to integrated sensory information from several sensory modalities. They suggest that the convergence of inputs from different sensory modalities within neural areas such as the superior colliculus appears to be a neural mechanism by which organisms integrate complex stimuli in their environment (Meredith & Stein, 1986a). Research with bobwhite quail chicks, (e.g., Experiment 1; Lickliter, 1990a, b; Lickliter 1994; Lickliter & Virkar, 1989; Sleigh & Lickliter, in press, a) has demonstrated that bobwhite quail display this intersensory functioning by 72 hrs. These studies have also shown that by altering chicks' sensory experience, this ability to integrate information from several sensory modalities can be accelerated or decelerated depending on the type of prenatal stimulation provided to the sensory systems. Since the avian brain contains a well developed superior colliculus region, it seems likely that sensory input stimulating this area of the brain might lead to accelerated intersensory functioning in bobwhite quail chicks. Future studies should use histological measures to examine patterns of neuronal development that result from various types of sensory experience, which could then be compared to the behavioral data.

In addition to examining the timing of experience, further studies should also examine the mechanisms by which the types of altered social experiences used in the present study lead to delayed intersensory responsiveness. For example, one critical aspect of altered tactile experience used in Experiment 2 involves the lack of movement. Importantly, the results from this experiment suggest that even when chicks are able to physically interact with siblings, their intersensory functioning may be altered when this physical interaction is with some static, non-interactive siblings. This raises the possibility that reciprocal interaction between members of a species, of which movement is a critical component, may be necessary for normal perceptual functioning. These findings also suggest that continuous exposure to normal, moving siblings during postnatal development is critical to subsequent intersensory functioning. Future studies should examine the role of movement in maintaining species-typical perceptual outcomes.

The current study demonstrated that differing types of rearing environments lead to differences in perceptual outcome. In this light, future studies might examine how either enriched or impoverished rearing conditions may affect perceptual development. Several studies have previously established that differences between both type and amount of stimulation at different ages affect developing behavioral patterns. For example, Renner and Rosenzweig (1986) reared juvenile rats (30 - 60 days of age) in enriched or impoverished environments. Rats in the enriched environments differed from those reared in the impoverished conditions by demonstrating more complex types of exploratory behavior. Renner (1987) extended this line of research by rearing adult rats in either enriched or impoverished conditions. After 30 days in these rearing conditions, each rat was tested in a dimly lit arena with objects and measured on both type and amount of exploratory behavior. Results revealed that rats reared in enriched conditions showed greater diversity of behavior, greater overall amounts of exploratory behavior, and demonstrated longer and more complex interaction with the objects placed in the arena. These findings highlight the importance of experiential influence on behavior, regardless of whether this experience occurs during childhood or adulthood. Future studies might examine whether these differences in rearing environments extend to avian species during both infancy and adulthood.

Another promising area of research involves examining the effects of differential rearing environments on developing neural structures. While the current study focused on behavioral outcomes related to different rearing experiences, future studies should examine how altered experience leads to neurological differences in sensory maps of developing organisms. Such studies would potentially forge a link between biological, behavioral, and social levels of scientific analysis by examining the neurological underpinnings of behavioral outcomes. Studies from several researchers using animal models have demonstrated that behavioral changes may be mediated by neurological reorganization that follows exposure to differential experiences. For example, Diamond and her colleagues have demonstrated that enriched environmental conditions may affect neural organization of developing organisms (Diamond, Johnson, Mizono, Ip, Lee, & Wells, 1977). Male Long-Evans rats were reared in either control, impoverished or enriched conditions. Following treatment, histological sections of their forebrains were examined at 26, 41, 108, or 650 days of age. Rats in each group were reared in one of these conditions from day 60-61, 60-64, or 60-90, thus exposing them to differential amounts of their rearing condition. Results revealed that rats reared in an enriched environment from 60-64 and 60-90 days displayed increased occipital and pyriform cortex thickness. Rats reared in impoverished environments demonstrated normal pyriform cortex but decreased occipital cortex thickness after the 30-day experiment, suggesting that the timing of experience is indeed important in some developing neural structures.

In a subsequent study, adult rats were exposed to either control or enriched environmental conditions at 112 days (Uylings, Kuypers, Diamond, & Veltman, 1978). This treatment was continued for 30 days, at which time both the frontal and occipital cortexes of subjects were examined to measure cortical growth. Findings revealed that subjects exposed to the enriched environments had significantly more dendritic branching and cortical thickening than controls, indicating that the enriched environment led to increased neuronal differentiation and growth. Because this study utilized adult subjects, it suggests that the timing of experience can potentially influence developmental processes at any stage of the developing organism's life (Uylings, *et al*, 1978).

In addition to the studies on mammalian species, several recent studies have examined neurological effects of altered experience in avian species. For example, Knudsen (1983) reared developing altricial barn owls with one ear plugged, which changed auditory input to both ears and altered the bird's auditory receptive fields in the optic tectum. The earplugs were removed when the owls became adults, and results revealed that the input from the previously deprived ear was far stronger than when the auditory map was first formed, which resulted in misaligned auditory and visual spatiotopic maps. Correction of these misaligned maps occurred if owls were allowed visual input, but if owls were reared in darkness, no corrective reorganization occurred (Knudsen, 1985). Thus an early experiences in perceptual input lead to changes at the neurological level which persist even into adulthood.

In sum, the present results highlight the importance of developmental constraints and normal sensory experience in maintaining species-typical perceptual outcomes, and further emphasize the dynamic nature of early perceptual functioning. Additionally, the current study highlights the behavioral plasticity of developing organisms and the role of experiential factors in shaping developmental trajectories. The developing organism's early social environment is rich with sensory information, which helps organize and shape species-typical perceptual preferences. The constraints of the organism's sensory systems interact with both the types and amounts of sensory information presented to the organism, as well as with the timing at which these types and amounts of stimulation are made available. An understanding of the nested relationship between these factors may eventually lead to a demarcation of the particular features of infants' sensory stimulative environments that lead to normal, species-typical behavioral outcomes.

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Table 1. Preference of Chicks in Simultaneous Auditory-Visual Choice Test in Experiment 1.

			Preference		
Age (in hrs)	n	n responding	Bobwhite Hen with Bobwhite Call	Scaled Hen with Bobwhite Call	No Preference
72	20	20	14*	2	4

* p < .01 (Chi-square test)

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

		Latency		Duration	
Age (in hrs)	n	Bobwhite Hen with Bobwhite Call	Scaled Hen with Bobwhite Call	Bobwhite Hen with Bobwhite Call	Scaled Hen with Bobwhite Call
72	20	64.25* (61.08)	216.25 (109.94)	132.65* (101.77)	16.95 (34.02)

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

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

			Preference		
Age (in hrs)	n	n responding	Bobwhite Hen with Bobwhite Call	Scaled Hen with Bobwhite Call	No Preference
72 HRS WITH FREEZE-DRIED SIBLINGS					
72	20	18	7	7	4
FIRST 36 HRS WITH FREEZE-DRIED SIBLINGS					
72	20	19	8	8	3
SECOND 36 HRS WITH FREEZE-DRIED SIBLINGS					
72	20	19	8	6	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 Call	Scaled Hen with Bobwhite Call	Bobwhite Hen with Bobwhite Call	Scaled Hen with Bobwhite Call
72 HRS WITH FREEZE-DRIED SIBLINGS					
72	20	108.20 (122.58)	131.20 (126.07)	81.15 (84.95)	65.30 (68.49)
FIRST 36 HRS WITH FREEZE-DRIED SIBLINGS					
72	20	140.00 (113.97)	149.95 (130.87)	85.50 (83.67)	72.70 (76.96)
SECOND 36 HRS WITH FREEZE-DRIED SIBLINGS					
72	20	130.25 (121.40)	108.85 (116.10)	62.95 (58.68)	84.95 (70.80)

Table 5. Percentages of Observation Time that Subjects Spent in Various Behavioral States at Two Observation Points in Experiment 2.

	Rearing Condition	
Behavior	Control	72 Hrs Altered Tactile
24 HRS FOLLOWING HATCHING:		
Eyes Open	82.27%	80.45%
Proximity	95.00%	93.64%
Contact	91.36%	85.91%
Synchrony	42.27%	40.45%
Walking	47.27%	52.27%
Contentment Calls	2.73%	6.82%
Distress Calls	4.55%	1.36%
Standing	51.36%	54.09%
Sitting	39.55%	30.91%
Lying	9.09%	15.00%
Pecking	4.55%	5.91%
Drinking	3.64%**	0.00%
Wing Flutters	7.27%**	25.45%
	n = 22	n = 22
48 HRS FOLLOWING HATCHING:		
Eyes Open	75.71%*	88.64%
Proximity	99.05%	99.55%
Contact	87.62%	98.18%
Synchrony	22.86%	24.55%
Walking	26.19%	36.36%
Contentment Calls	2.38%	1.36%
Distress Calls	0.00%	0.00%
Standing	47.62%**	84.55%
Sitting	43.81%**	13.64%
Lying	8.57%*	1.36%
Pecking	4.29%	5.45%
Drinking	0.00%	0.00%
Wing Flutters	5.24%*	16.82%
	n = 21	n = 22

* (p < .05, independent t-test) ** (p < .01, independent t-test)

Table 6. Righting Response (in Seconds) for Subjects in Each Rearing Condition at 48 Hrs in Experiment 2.

Rearing Condition	n	M	SD	Range
Control	21	1.51	2.12	0.41 - 10.06
72 Hrs Altered Tactile	22	1.32	2.95	0.31 - 14.47

Table 7. Preference of Chicks in Simultaneous Auditory-Visual Choice Tests in Experiment 3.

			Preference		
Age (in hrs)	n	n responding	Bobwhite Hen with Bobwhite Call	Scaled Hen with Bobwhite Call	No Preference
72 HRS WITH DISEMBODIED CHICK CALLS					
72	20	18	9	6	3
FIRST 36 HRS WITH DISEMBODIED CHICK CALLS					
72	20	20	10	8	2
SECOND 36 HRS WITH DISEMBODIED CHICK CALLS					
72	20	20	10	7	3

Table 8. Means and Standard Deviations of Latency and Duration Scores of Chicks in Simultaneous Auditory-Visual Choice Tests in Experiment 3.

		Latency		Duration	
Age (in hrs)	n	Bobwhite Hen with Bobwhite Call	Scaled Hen with Bobwhite Call	Bobwhite Hen with Bobwhite Call	Scaled Hen with Bobwhite Call
72 HRS WITH DISEMBODIED CHICK CALLS					
72	20	164.80 (117.28)	162.05 (105.90)	53.15 (56.40)	53.95 (62.73)
FIRST 36 HRS WITH DISEMBODIED CHICK CALLS					
72	20	168.25 (119.09)	175.85 (122.47)	57.80 (73.09)	54.95 (60.56)
SECOND 36 HRS WITH DISEMBODIED CHICK CALLS					
72	20	141.60 (118.84)	122.95 (111.95)	76.65 (75.97)	67.15 (67.21)

Table 9. Preference of Chicks in Simultaneous Auditory-Visual Choice Tests in Experiment 4A.

			Preference		
Age (in hrs)	n	n responding	Bobwhite Hen with Bobwhite Call	Scaled Hen with Bobwhite Call	No Preference
72 HRS REARED IN DARKNESS					
72	20	20	6	11	3
FIRST 36 HRS REARED IN DARKNESS					
72	20	18	9	8	1
SECOND 36 HRS REARED IN DARKNESS					
72	20	19	12*	3	4

* P < .05 (Chi-square test)

Table 10. Means and Standard Deviations of Latency and Duration Scores of Chicks in Simultaneous Auditory-Visual Choice Tests in Experiment 4A.

		Latency		Duration	
Age (in hrs)	n	Bobwhite Hen with Bobwhite Call	Scaled Hen with Bobwhite Call	Bobwhite Hen with Bobwhite Call	Scaled Hen with Bobwhite Call
72 HRS REARED IN DARKNESS					
72	20	128.80	99.60	43.50	77.95
		(131.30)	(99.97)	(69.02)	(83.25)
FIRST 72 HRS REARED IN DARKNESS					
72	20	197.25	180.65	56.50	75.10
		(123.70)	(121.90)	(80.45)	(99.85)
SECOND 72 HRS REARED IN DARKNESS					
72	20	69.90*	161.00	128.90*	55.60
		(101.35)	(127.71)	(97.96)	(76.35)

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

Table 11. Preference of Chicks in Simultaneous Color-Choice Test in Experiment 4B.

Age (in hrs)	n	n responding	Preference Red Dot	 Blue Dot
CONTROL CHICKS				
72	20	0	0	0
72 HRS REARED IN DARKNESS				
72	20	0	0	0

Date ______________ Time _____________ Subject _______

Condition ________________ Hatchdate _____________ Observer _______________

Time	S/W	Prox	Cont	Sync	Mve	Voc Con	Voc Dis	Sd/L/ Sit	Peck	Drnk	Wing Flutr	
00												
01												
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09												
Righting			Date died									

Date _________________ Time ___________ Observer _________________

Time	S/W	Prox	Cont	Sync	Mve	Voc Con	Voc Dis	Sd/L/ Sit	Peck	Drnk	Wing Flutr	
00												
01												
02												
03												
04												
05												
06												
07												
08												
09												
Righting			Date died									

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1989 - 1991

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1994 - 1995

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Additional duties include coordinating ongoing research projects, and managing and maintaining laboratory facilities.
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1994 - 1996

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Trained, supervised, and evaluated graduate teaching assistants.
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Created syllabi and lesson plans, constructed and analyzed tests.
Managed department subject research pool.
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Sleigh, M.J., Columbus, R.F., & Lickliter, R. (in press). Type of prenatal sensory experience affects prenatal auditory learning in bobwhite quail. Journal of Comparative Psychology.

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PAPERS PRESENTED AT SCIENTIFIC MEETINGS:

Columbus, R.F. & Lickliter, R. Modified postnatal social experience alters intersensory development of bobwhite quail chicks. To be presented at the International Society for Developmental Psychobiology Annual Meeting, Washington, DC, November, 1996.

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

Lickliter, R., Lewkowicz, D.J., & Columbus, R. Role of spatial contiguity in quail chicks' responsiveness to multimodal maternal cues. Presented at the International Conference for Infant Studies, Providence, RI, April 1996.

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

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.

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