

Introduction

Recently, there has been a growing interest in developmental psychology in explaining the processes and mechanisms by which humans and animals learn the varied associations between stimuli within their specific ecological niche (DeCasper & Fifer, 1980; DeCasper & Spence, 1986; Gottlieb, Tomlinson, & Radell, 1989; Lariviere & Spear, 1996; Lickliter & Hellewell, 1992; Poeggel & Braun, 1996; Reed, 1996; Sleight, Columbus, & Lickliter, 1996; Smotherman & Robinson, 1985; Tees, Buhrmann, & Hanley, 1990). Research conducted within this approach is typically designed to accumulate detailed information about the ways in which animals and humans adapt to their natural environments by means of learning (Gottlieb, 1983; Johnston, 1981, 1985; Lickliter, 1996; Reed, 1996).

Specifically, this ecological systems approach to learning emphasizes examining, describing, and understanding behavior as it occurs within a particular ecological setting. Within this approach, the goal is not simply to show that animals can learn under some circumstances. Instead, the focus is on how species-typical environmental conditions and patterns of organismic development lead to similar learning patterns across all or most members of a particular species as part of adaptation to their specific environmental circumstances (Johnston, 1985). Therefore, this approach views learning processes as fitting into a larger comparative, evolutionary perspective to behavior change and development (Gottlieb, 1985). In addition, the ecological approach emphasizes that learning is a mechanism by which organisms adapt to their surround, but it does not preclude laboratory experiments as means by which learning can be studied. In fact, Johnston (1985) has stated that little can be understood about learning without experimentally altering the conditions under which it normally occurs. However, the goal is to ensure the hypotheses being tested are designed to examine the development of learning strategies within the species-typical course of an animal's life, thus taking a more ethological approach to the study of learning (Gottlieb, 1985; Johnston, 1985; Timberlake, 1990; Tinbergen, 1951).

I. ECOLOGICAL PERSPECTIVE OF LEARNING CAPACITY

Before examining the particulars of an ecological perspective, it is necessary to fit this perspective into a larger framework of learning theory and research. The ecological approach to learning arose from questions that remained unanswered by more traditional approaches, which held the underlying assumption that general learning processes can be understood independent of specific forms of behavior change in specific environments and species. Specifically, this traditional approach to learning holds the underlying assumption that processes of learning differ from "instincts" inherent in various organisms, a view originally proposed by Thorndike that has endured across the past century of learning research (Domjan, 1998; Lorenz, 1969; Skinner, 1966). According to this view, learning processes cannot be studied in the presence of cues that evoke species-typical, or "instinctual" behaviors, as these instinctual reactions potentially interfere with "pure" learning processes. Given this learning – instinct dichotomy, research conducted within a traditional learning perspective has historically examined early learning ability within a laboratory environment, in which learning processes have been experimentally

examined in the absence of cues normally present within a particular organism's specific environmental niche. Thus, research conducted under the assumption that learning and instinctual processes are separate seek to separate a given organism from stimuli present within its species-typical environment, to remove the influence of instincts from learning processes (Johnston, 1985; Lickliter, 1996).

Research spanning the last 30 years has demonstrated that the fundamental assumption that learning (or experience) and instinct (or genetic influences) can be separated is conceptually flawed (Gottlieb, 1983, 1985; Lehrman, 1970; Miller & Blaich, 1984). For example, early studies of taste aversion revealed that all possible stimuli are not equally associable, thus contradicting traditional learning theories (Domjan, 1998; Lickliter, 1996; Seligman, 1970). Further, results from studies of maze running (Timberlake, 1983), song-learning (Eales, 1985), imprinting (Johnston & Gottlieb, 1981; Lickliter & Gottlieb, 1985, 1986, 1988), species-specific defense reactions (Bolles, 1970; Overmier & Seligman, 1967), foraging behavior (Shettleworth, 1972, 1975, 1983), and taste aversions (Rozin & Kalat, 1971) have contradicted the notion that learning can occur within a vacuum, apart from the influences of prior experience, context, and patterns of biological organization inherent to a particular species. These findings stimulated a movement among several researchers to view patterns of learned behavior as species-specific, experience-dependent, and specialized adaptations bounded by the environment in which animals develop.

In light of this increasing body of contradictory findings to traditional learning theory, Johnston (1985) proposed that an ecological framework which addresses these environmental and organismic influences on learning is necessary to more fully understand learning mechanisms in developing organisms. According to Johnston's (1985) proposal, there are six primary issues that characterize an ecological approach to learning as different from more traditional approaches. First, the task to be learned by any organism within a certain environment must be described, and this description must include an analysis of behavior patterns by which the animal interacts with its environment. From the ecological perspective, learning is the process by which an animal modifies its behavior within an environment, as a result of its own individual experience with that environment. Therefore, the task should be described in terms of how particular behaviors might be modified by experience (Johnston, 1985).

Second, an ecological approach to learning emphasizes that the organism interacts with its environment in an ongoing, reciprocal relationship. In this view, learning results from modification of the relationship between organism and environment (Germana, 1989; Johnston, 1985). Importantly, both organism and environmental characteristics change through time, suggesting that the nature of learning might also change during the course of individual development. Therefore, the ecological approach lends itself to developmental analysis of behavior change as a result of an ongoing, changing relationship between a changing environment and an adaptive organism.

Third, an ecological approach to learning seeks to describe not only the task to be learned, and the relationship between the organism and the environment, but also a description of the environment in which learning will potentially take place (Johnston, 1985). This would include a wealth of extraorganismic variables, such as conspecifics (i.e., single vs. multiple siblings), sensory stimulation (i.e., maternal calls, songs, etc.),

and contextual features (i.e., brood size), to name but a few. These variables potentially allow for differing learning opportunities at various stages of the life cycle.

The ecological approach also appreciates that learning occurs within a developmental system, as an individual's behavior changes in response to the challenges and opportunities of particular environmental niches (Gottlieb, 1985; Johnston, 1981, 1985; Lickliter, 1996, in press; Miller, 1997). According to this view, learning of specific behaviors and tasks occurs as a result of external influences (i.e., stimuli present within an ecological niche) and internal influences (i.e., status of sensory system development, physiological organization, experiential history) that are characteristic of individual organisms at any given point in development. In other words, what is learned by a developing organism is a function of both the stimuli present at a particular time in a specific environment in which the organism is living, and the organism's experiential history with those stimuli present within the environment.

Finally, the ecological framework allows for the study of learning to fit into the larger, evolutionary perspective of behavior change within and across various species. According to this view, learning is one means by which animals adapt to their natural environments. Since both animals and environments evolve over time, an ecological approach allows us to not only study the adapting animal, but also the environment to which the animal adapts. Unlike traditional learning perspectives, the ecological perspective does not preclude developmental (ontogenetic) or evolutionary (phylogenetic) analyses of behavior change as a result of learning processes, and as such, allows for a broader definition of learning than has traditionally been accepted (Johnston, 1985).

In sum, the ecological approach to learning holds that species-typical patterns of behavior can result from learning, rather than instinctual, processes; that organisms interact with specific stimuli in their environments, which leads to behavior change over the course of individual development; that both internal organismic factors and external environmental factors interact through the learning process; and that species-level evolutionary change can result from patterns of behavior learned by many individuals that are transmitted to subsequent generations. In summary, this perspective assumes that associations and behaviors are learned during individual development, and are constructed from the organism's interaction with stimuli present within its environment throughout out the organism's experiential history.

II. EVIDENCE FOR EXPERIENCE-DEPENDENT CONSTRUCTION OF LEARNING CAPACITY

Developmental psychologists have increasingly turned their attention to the processes and mechanisms that influence the relationship between organisms and their specific environmental niches. Because biological systems are continually changing, the experiences that organisms create and encounter can influence developmental processes and modify developmental outcomes. One important finding that has repeatedly emerged from this line of research is that, for most animal species, experience plays a critical role in the development of perceptual, social, and cognitive processes (Capitanio, 1984; Gottlieb, 1997; Johnston, 1987; King & West, 1987; Lickliter, Dyer, & McBride, 1993; Miller, 1997; Spear & Molina, 1987). 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 understanding the typical experience of any organism is crucial to understanding how particular phenotypic traits or characteristics emerge in development (King & West, 1987; Lickliter & Berry, 1990; West & King, 1987). From this view, the minimal 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, 1996, in press; Oyama, 1985; West & King, 1987).

For example, research has revealed that human infants prefer familiar stimuli that they have encountered within their particular developmental niche. DeCasper and Fifer (1980) demonstrated that human infants prefer to listen to their mother's voice over an unfamiliar female voice in the period immediately following birth. These findings suggest that infants prefer the form of auditory stimulation they heard and experienced in the period prior to birth. In an experimental study, DeCasper and Spence (1986) asked pregnant mothers to read a story to their unborn infants during the period prior to birth. Results revealed that following birth, infants preferred to listen to recordings of the familiar stories over unfamiliar stories.

Poeggel and Braun (1996) studied patterns of perceptual learning in the degu (*Octodon degus*), a small South American rodent, during period prior to and following birth. Results revealed that two-week-old pups from normally vocalizing mothers expressed a preference for the maternal call, in contrast to pups from surgically muted mothers. Importantly, degu mothers utter specific maternal calls during nursing that stimulate and reinforce suckling. Pups from surgically muted mothers demonstrated decreased suckling behavior and slower weight gain than pups from vocalizing mothers. Finally, neurological findings indicate that pups from normally vocalizing mothers exhibit increased activity in the prefrontal cortex, an area known to be involved with associative learning processes, when listening to the familiar maternal call. In contrast, pups from muted mothers demonstrated reduced prefrontal activity when exposed to the maternal call, suggesting a functional learning deficit that resulted from lack of experience with the maternal vocalizations during nursing.

Research with precocial avian species, or those whose sensory systems are fully functional at birth, has also demonstrated that early experience can affect subsequent perceptual preferences. For example, bobwhite embryos who have experienced a particular variant of a bobwhite maternal call for 24 hrs prior to hatching prefer this call at 24 hrs following hatching over a different, unfamiliar bobwhite maternal call (Lickliter & Hellewell, 1992). Similarly, chicks who have been exposed to a particular maternal call in the period following hatching prefer this call over a different maternal call at 72 hrs of postnatal age (Columbus & Lickliter, 1997).

These studies examining the effects of early experience on subsequent perceptual preference have reliably demonstrated that sensory stimulation present within the developing organisms' ecological niche can influence what is learned by the organism. Recently, investigators have turned their attention to how organismic factors also affect the learning process. In light of the ecological framework proposed by Johnston (1985), several researchers utilizing this approach have sought to examine how constraints inherent to the organism helps determine both the functions and development of learning processes (Gottlieb, 1971, 1983, 1993; Johnston, 1981, 1985; Klein & Mowrer, 1989;

Lickliter, 1996; Lickliter & Hellewell, 1992). Research within this area of psychology has demonstrated that what is learned by organisms is bounded not only by the environmental stimuli within the organism's niche, but also by the perceptual capacity of the organism at any given point in development.

For example, previous research has shown that the sensory systems of birds and mammals do not become functional at the same time in development (Gottlieb, 1971). Based on this sensory system hierarchy, several researchers have suggested that competition within and between the sensory systems may regulate the development of emerging perceptual capabilities. Specifically, Turkewitz and Kenny (1982) have proposed that because the sensory systems are linked throughout perinatal development, modifications of sensory experience to one modality may interfere with the development of earlier or later developing sensory systems.

Previous studies of learning in animal infants have indicated that changes in perceptual learning capacities correspond to the sequence of onset of sensory function. For example, Lickliter and Hellewell (1992) found that bobwhite embryos exposed to an individual bobwhite maternal call during the 24 hrs prior to hatching could learn and remember this call for 24 hrs post-hatching. However, chicks exposed to this same call during the 24 hrs following hatching could not learn the maternal call. In a similar study, Radell and Gottlieb (1992) found that augmented stimulation from an earlier developing sensory system (i.e., vestibular) can interfere with auditory learning (a later developing sensory system), if the amount of earlier-developing stimulation provided falls outside some optimal range. Finally, Sleight, Columbus, and Lickliter (1996) found that bobwhite quail embryos exposed to various types of auditory stimulation during prenatal development were differentially able to learn an individual bobwhite maternal call. In sum, these studies have demonstrated that attenuated or augmented types of prenatal stimulation can affect developing avian embryos' ability to learn auditory information.

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 → chemical → auditory → and visual, Gottlieb, 1971; Mistretta & Bradley, 1978). 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, as well as learning capacity, in developing organisms. Most studies within this line of research have addressed this issue by either adding or taking away sensory stimulation at specific times in prenatal or postnatal development (Banker & Lickliter, 1993; Columbus & Lickliter, 1997, 1998; Lickliter, 1990a, 1990b, 1994; Lickliter & Hellewell, 1992; Lickliter & Lewkowicz, 1995; Sleight & Lickliter, 1995, 1996, 1997).

This line of research has also demonstrated that within any organisms' ecological niche, the particular types, amounts, and timing of sensory stimulation can effectively shape perceptual functioning and learning capacity during both prenatal development (Lickliter, 1990a, 1990b; Lickliter & Lewkowicz, 1995; Sleight, Columbus, & Lickliter, 1996) and during postnatal periods (Columbus & Lickliter, 1998; McBride & Lickliter, 1993, 1994). Specifically, sensory stimulation that falls within some species-specific optimal range leads to species-typical patterns of perceptual functioning and learning capacity, whereas sensory stimulation that falls outside an optimal range can lead to

deficits in species-typical developmental outcomes. In addition, when these specific experiences are encountered during development can also affect perinatal perceptual functioning and learning ability (Lickliter & Hellewell, 1992; Sleigh & Lickliter, 1998).

In light of research examining the biological constraints of learning and perceptual functioning, 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, how perceptual hierarchies organize and reorganize, and how learning capacity is linked to sensory system functioning throughout the developmental process. In a similar vein, Lickliter (1993) has suggested that the type, timing, and amount of developmental events also impose constraints as well as opportunities for the developing organism.

Research on learning in rat pups has demonstrated that there are developmental differences in sensory conditioning and sensory integration that correspond to the sequence of sensory system development and the rat's developmental age. Specifically, Spear and McKinzie (1994) report that as ontogeny progresses, rat pups become better able to differentiate compound stimuli (where the stimuli from two different sensory modalities are presented together) as they have increasing experience with these compound stimuli and their sensory systems become differentiated. In addition, rat pups are better able than adults to process both intersensory information (from two separate sensory modalities) and intrasensory information (within the same sensory modality). This finding suggests that the timing of presentation of sensory information may affect early associative learning capacity in rats (Spear & McKinzie, 1994).

III. EXAMPLE: SPECIES-TYPICAL LEARNING PATTERNS IN PRECOICIAL AVIAN SPECIES

Like most vertebrates, precocial birds exhibit behavioral and perceptual plasticity that is influenced by sensory features available within their developmental context. In other words, chicks' sensory experiences can modify their species-typical patterns of development. As previously discussed, the sensory systems of birds and mammals do not become functional at the same point in development, which implies that competition within and between sensory systems may regulate the development of emerging perceptual capabilities. Turkewitz and Kenny (1982) originally proposed a developmental intersensory interference hypothesis, which suggested that because sensory systems are linked throughout perinatal development, modifications of sensory experience from one modality can interfere with the development of an earlier or later developing sensory system. For example, premature stimulation of a later developing sensory system (i.e., visual) potentially interferes with normal functioning of an earlier developing system (i.e., auditory, vestibular). This interference may lead to deficits or disorders in normal perceptual development (Gottlieb, Tomlinson, & Radell, 1989; Lickliter, 1990a, 1990b; Radell & Gottlieb, 1992; Turkewitz & Kenny, 1982). This sequential order of sensory system functioning necessarily provides limitations on sensory input to the various modalities throughout development. However, far from being a detriment to normal sensory development, this pattern of onset may decrease competition between the developing sensory systems, which leads to normal

development for each sensory system (Turkewitz & Devenny, 1993; Turkewitz & Kenny, 1982, 1985; Turkewitz & Mellon, 1989).

Previous studies of learning in animal infants have indicated that ontogenetic changes in perceptual learning capacities are influenced by the sequence of onset of sensory function (Columbus & Lickliter, 1997; Gottlieb, Tomlinson, & Radell, 1989; Lickliter & Hellewell, 1992; Lickliter & Lewkowicz, 1995; Radell & Gottlieb, 1992; Sleigh, Columbus, & Lickliter, 1996; Sleigh & Lickliter, 1995). This body of research has provided evidence that, depending on the experiential status of a particular sensory system at a given point in development, the organism's learning capacity is constrained by input to different sensory modalities as well as by the level of maturation of that sensory system. In particular, this work has demonstrated that infants' early learning capacity is mediated by the type, amount, and timing of sensory stimulation available within the developing organism's species-typical niche.

Timing of Stimulation

To test Turkewitz and Kenny's (1982) hypothesis that earlier than normal sensory stimulation potentially interferes with developing sensory modalities, Gottlieb, Tomlinson, and Radell (1989) examined the effects of early auditory and visual experience on perinatal learning ability in duckling embryos and hatchlings. Under normal conditions, mallard embryos are able to learn a particular maternal call and demonstrate a preference for the familiar call in a simultaneous choice test following hatching (Gottlieb, 1988). In this study, duckling hatchlings were exposed to a maternal assembly call during either prenatal or postnatal development and tested their preference for that same call versus an unfamiliar call of the same species. Findings revealed that ducklings who heard the call during the 24 hrs following hatching showed a significant preference for that familiar call, regardless of whether they had been prenatally incubated in lighted or darkened incubators. However, embryos which were exposed to the call during the 24 hrs prior to hatching in lighted conditions failed to learn the maternal call, while embryos reared in darkened conditions were able to learn the call. In addition, embryos which received premature visual experience non-concurrently with the auditory stimulation preferred the familiar call, whereas embryos who were exposed to the light concurrently with the call could not learn that call (Gottlieb, Tomlinson, & Radell, 1989). These findings suggest that premature visual stimulation only interferes with auditory learning when the visual stimulation is presented concurrently with the auditory information to be learned, and thus seem to support Turkewitz and Kenny's model of intersensory interference.

Recent research with bobwhite quail chicks has provided additional evidence supporting Turkewitz and Kenny's (1982) "limitations" hypothesis. For example, Lickliter and Hellewell (1992) examined the ability of bobwhite quail embryos and hatchlings to learn an individual bobwhite maternal call during prenatal and postnatal development. Results revealed that bobwhite chicks show no naïve preference for two individual variants of a bobwhite maternal call (Call A or Call B). However, embryos who received 10 min/hr exposure to Call B during the 24 hrs prior to hatching significantly preferred this familiar call at 24 hrs following hatching. In contrast, chicks tested at 48 hrs did not appear to retain a preference for this familiar call for 48 hrs following exposure (Lickliter & Hellewell, 1992), indicating that bobwhite embryos are

capable of learning and remembering a specific maternal call for at least 24 hrs following hatching.

[Figure 5. Chicks.jpg \(32KB\)](#)

Further experiments in this study revealed that bobwhite chicks who received postnatal exposure to bobwhite maternal Call B during the first 24 hrs following hatching did not demonstrate a significant preference for this familiar call at either 48 or 72 hrs following hatching. This finding indicated that perhaps the learning process is influenced by the context in which auditory stimulation is provided to developing organisms. To examine this possibility, Lickliter and Hellewell (1992) reared chicks in physical isolation following hatching, thus attenuating their visual and social experience, and provided them with 10 min/hr of bobwhite maternal Call B for the first 24 hrs following hatching. Results from this experiment revealed that isolation-reared chicks were able to learn and remember the familiar Call B at 48 hrs of postnatal age, unlike socially-reared chicks, suggesting that sensory interference normally present in postnatal rearing conditions interferes with bobwhite hatchlings' ability to learn auditory information in the days following hatching. A final experiment in this study examined this sensory-interference hypothesis by providing embryos with 10 min/hr of prenatal patterned visual stimulation in addition to the 10 min/hr of bobwhite maternal Call B either concurrently or non-concurrently. Results showed that concurrent visual and auditory stimulation leads to chicks' inability to learn the maternal call, while non-concurrent visual and auditory stimulation resulted in auditory learning (Lickliter & Hellewell, 1992).

Results from Lickliter and Hellewell (1992) provide the following evidence supporting a biological constraints model of perceptual learning: first, visual and auditory stimulation provided by social experience during early postnatal development can interfere with hatchlings' ability to learn auditory information during the days following hatching. Second, prenatal visual stimulation provided concurrently with auditory stimulation appears to compete for the embryo's attention to the auditory information, leading to deficits in auditory learning capacity during prenatal development. Finally, non-concurrent auditory and visual stimulation decrease competition between these sensory systems during the prenatal period, allowing successful auditory learning during the 24 hrs prior to hatching.

Amount of Stimulation

To study the effects of overall amount of stimulation on auditory learning, Radell and Gottlieb (1992) exposed duckling embryos to augmented prenatal vestibular stimulation (by placing the eggs on waterbeds) to examine the effects of augmented stimulation of an earlier-developing sensory system (i.e., vestibular) on a later-developing system (i.e., auditory). The augmented vestibular stimulation was presented either concurrently or non-concurrently with presentation of an individual duckling maternal call. Ducklings' preferences for the familiar auditory information were subsequently tested. Findings revealed that concurrent stimulation of the vestibular and auditory systems led to deficits in auditory learning, while non-concurrent sensory stimulation did not compromise ducklings' learning ability. However, when additional postnatal auditory stimulation was provided to ducklings who had received concurrent

stimulation prenatally, hatchlings were able to learn the call. Importantly, Radell and Gottlieb (1992) found that overall reduced amounts of prenatal concurrent stimulation did not interfere with prenatal auditory learning ability, suggesting that stimulation which falls within some optimal range does not lead to deficits in embryos' ability for perceptual learning.

These findings have been supported by more recent examinations of auditory learning capacity in bobwhite quail embryos. Presumably, if Radell and Gottlieb's (1992) theory that sensory stimulation that falls within some optimal range leads to successful auditory learning, amounts of stimulation that fall outside this optimal range should lead to deficits in perceptual learning capacity in embryos. To examine this possibility, Sleigh and Lickliter (1995) provided bobwhite quail embryos with substantially augmented (40 min per hour) prenatal visual stimulation nonconcurrently with 10 min/hr of bobwhite maternal Call B. Results revealed that, in fact, this substantially increased amount of sensory stimulation led to failure of bobwhite embryos to demonstrate a significant preference for Call B at 24 hrs following hatching, a result seen in previous studies with unmanipulated chicks (Lickliter & Hellewell, 1992). The results from this study suggest that substantially increasing the amount of sensory stimulation in the prenatal environment can indeed lead to deficits in early auditory learning capacity.

In a similar vein, Lickliter and Lewkowicz (1995) recently demonstrated that substantially attenuated prenatal sensory stimulation also appears to interfere with prenatal auditory learning. In this study, bobwhite quail embryos were incubated either communally or in isolation from their broodmates and were exposed to 10 min/hr of bobwhite maternal Call B. Results showed that chicks reared communally demonstrated successful auditory learning at 24 hrs following hatching, paralleling results from unmanipulated embryos (Lickliter & Hellewell, 1992). In contrast, embryos incubated in isolation did not show a significant preference for the familiar Call B at 24 hrs, suggesting that physical isolation from broodmates removed the normally present background stimulation that is necessary for successful auditory learning. In a further experiment, Lickliter and Lewkowicz (1995) reared embryos in physical isolation from their broodmates, but in addition provided them with 10 min/hr of concurrent visual stimulation for the 24 hrs prior to hatching. While previous studies have shown that increased amounts of prenatal stimulation lead to deficits in auditory learning (Radell & Gottlieb, 1992; Sleigh & Lickliter, 1995), it has also been demonstrated that stimulation that falls within some optimal range allows for the development of successful learning. Therefore, Lickliter and Lewkowicz reasoned that increasing the arousal level of embryos reared in isolation by providing them with 10 min/hr of augmented patterned prenatal visual stimulation (to substitute for the attenuated tactile and vestibular stimulation provided by broodmates) would enable embryos to learn a specific maternal call. In fact, embryos reared in isolation with 10 min/hr of concurrent visual stimulation and 10 min/hr of bobwhite maternal Call B nonconcurrently did show a significant preference for Call B at 24 hrs following hatching. This result suggests that prenatal learning requires some optimal level of background stimulation to be effective (Lickliter & Lewkowicz, 1995), a conclusion that has also been supported in other studies of developmental intersensory interference and learning capacity (Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992; Sleigh & Lickliter, 1995).

Type of Stimulation

In addition to the timing and amount of stimulation, the type of stimulation available within developing organisms' context or milieu has been found to affect early perceptual learning capacity. For example, Sleigh, Columbus, and Lickliter (1996) recently examined the effects of specific types of prenatal auditory stimulation on the auditory learning capacity of bobwhite embryos. In this study, embryos were incubated in either social or isolation conditions, and were exposed to either embryonic contentment or distress calls in addition to 10 min/hr of bobwhite maternal Call B. Results revealed that socially incubated embryos could learn Call B, whereas embryos denied tactile and visual stimulation by isolation-rearing were unable to learn this call. Chicks exposed to bobwhite chick contentment calls, in addition to Call B, were able to learn the maternal call, regardless of whether they were reared in isolation or communally. On the other hand, embryos reared with exposure to bobwhite chick distress calls in addition to Call B were unable to learn this call, whether they were reared in isolation or socially. These findings suggest that the type of stimulation the developing organism encounters within its prenatal environment can affect normal perceptual learning ability (Sleigh, Columbus, & Lickliter, 1996).

Taken together, this line of research with precocial avian embryos and infants provides evidence that attenuated or augmented types of prenatal stimulation, presented at different times during perinatal development, can affect developing embryos' ability to learn and remember auditory information. In the larger arena of learning theory and research, these studies provide a growing body of evidence that supports an ecological approach to understanding early learning processes. In particular, it appears that characteristics of the developing organism, such as interactions between sequentially developing sensory systems, coact with characteristics of the organism's ecological niche, such as type, amount, and timing of sensory stimulation, to determine early perceptual learning capacity.

Most studies outlined thus far have led to a greater understanding of prenatal determinants of learning capacity, there have been few examinations of perceptual learning following birth or hatching. In particular, most of the reviewed studies have focused on embryos' and hatchlings' learning capacity within the 24 hr prior to and following hatching. They have also tended to focus on how external characteristics found within the developing organism's environment affect early learning ability. What remains to be explored is how organismic factors, interacting with various forms of external stimulation, affect early postnatal learning capacity. In other words, what these studies have undercharacterized or failed to adequately explore is how learning capacity changes throughout early development, depending on the status of the developing sensory modalities and the changing contextual conditions from prenatal to postnatal life.

In a recent study, Columbus and Lickliter (1997) found preliminary evidence that patterns of postnatal learning are different from prenatal learning in bobwhite quail. Previous studies have shown that embryos who have been incubated socially and exposed to an individual maternal bobwhite maternal call during the 24-36 hrs immediately prior to hatching, can reliably learn this call and remember it for at least 24 hrs following exposure (Lickliter & Hellewell, 1992; Lickliter & Lewkowicz, 1995; Sleigh, Columbus, & Lickliter, 1996). To test for differences in postnatal learning ability, Columbus and

Lickliter exposed hatchlings to 10 min/hr of bobwhite maternal Call B during following hatching in either lighted or light-attenuated postnatal conditions, and tested chicks for their preference for the familiar Call B over an unfamiliar maternal Call A at 24, 48, 72, or 96 hrs. Call A and Call B were recorded in the field, and are similar in phrasing, call duration, repetition rate, dominant frequency, and frequency modulation (see Heaton, Miller, & Goodwin, 1978 for acoustical details).

[Figure 3. bwcalla.aiff \(660KB\)](#)

[Figure 4. bwcallb.aiff \(537KB\)](#)

Findings from this study revealed that socially reared chicks demonstrated no naïve preference for Call A or Call B at 24, 48, 72, and 96 hrs following hatching, suggesting that Call A and Call B were equally attractive to hatchlings at all ages tested following hatching. However, subjects who received exposure to 10 min/hr of Call B in lighted conditions from hatching until testing at 24, 48, 72, or 96 hr ($n = 20$ in each group), demonstrated a preference for Call B at 72 and 96 hrs following hatching. Chicks demonstrated a statistically significant preference for Call B at 48 hrs following hatching, but measures of latency for chicks in this group (as measured by the Wilcoxon signed-ranks test) did not support this pattern of preference. In other words, chicks' patterns of preference for the familiar Call B were weaker at 48 hrs than at 72 and 96 hrs following hatching, indicating that chicks' perceptual preference for the familiar strengthened with increasing amounts of exposure to Call B.

In light of findings from Lickliter and Virkar (1989), these findings seemed odd. Since chicks typically demonstrate auditory sensory dominance during the first 48 hrs of postnatal development, it would seem likely that chicks should be able to learn auditory information more quickly than 72 hrs when reared in lighted conditions. In addition, the ability to learn a specific maternal auditory call in the early days following hatching (i.e., by 24 hrs) would appear to have great ecological advantage for chicks' survival in natural conditions. However, our findings contrasted with what would be expected, in that chicks reared in lighted conditions were only able to learn the maternal call by 48-72 hrs following hatching (Columbus & Lickliter, 1997).

Previous studies of auditory learning in bobwhite quail chicks would suggest that chicks who receive exposure to a particular bobwhite maternal call can learn this call within 24 hrs of exposure (i.e., Lickliter & Hellewell, 1992; Lickliter & Lewkowicz, 1995). Results from this study seemed to contradict these earlier studies, in that chicks in this experiment were not able to successfully learn the bobwhite maternal call to which they had been exposed until 72 hrs following hatching.

It is important to note that in these earlier studies, bobwhite embryos were exposed to maternal auditory stimulation during the 24 hrs immediately prior to hatching, during prenatal development. Importantly, this time period marks when the chick's auditory system normally becomes regularly stimulated following the embryo's emergence into the air space of the egg, and visual system experience is limited by the presence of the egg. When these results are viewed in light of sensory system development and competition between the emerging auditory and visual systems, the present results would appear to suggest that some fundamental difference exists between prenatal and postnatal patterns of auditory learning in bobwhite quail embryos and

chicks. The obvious difference between prenatal and postnatal development in bobwhite quail is that following hatching, the visual system begins to receive input and becomes functional. Since chicks require 72 hrs to successfully learn auditory information during the postnatal period, it seems possible that visual system experience potentially interfered with chicks' ability to process auditory information, and thus interfered with postnatal auditory learning. In other words, because of increased competition from the later-developing visual system, chicks required a longer time period and more experience with auditory stimulation to learn maternal auditory information than embryos require during the prenatal period. Based on this hypothesis, we reasoned that attenuating visual experience following hatching should alleviate interference between the auditory and visual systems, which would result in chicks successfully learning auditory information.

Therefore, chicks were socially reared and placed in a darkened portable brooder from hatching until testing at 24, 48, 72, or 96 hrs following hatching ($n = 20$ in each group) to attenuated their experience with visual stimulation. 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. We could not be sure that this manipulation eliminated all visual experience for each subject, but the dark rearing condition drastically attenuated normal visual experience for the hatchlings. Subjects were tested at 24, 48, 72, or 96 hrs following hatching, in a simultaneous choice test between two individual bobwhite maternal calls (Call A and Call B).

Findings revealed that chicks reared in postnatal light-attenuated conditions demonstrated no naïve preference for Call A or Call B at 24, 48, 72, and 96 hrs following hatching. However, chicks reared in postnatal light-attenuated conditions following hatching and exposed to 10 min/hr of an individual bobwhite maternal Call B demonstrated a significant preference for this familiar call at 24, 48, 72, and 96 hrs following hatching (Columbus & Lickliter, 1997). These results suggest that chicks who are denied postnatal visual experience can successfully learn auditory information more quickly than chicks who are reared with normal visual stimulation postnatally. Importantly, these results support Turkewitz and Kenny's (1982) sensory system interference hypothesis, in that limitations on visual system experience (a later-developing sensory system) enable chicks to process and learn auditory information (from an earlier-developing sensory system).

The results from this preliminary study (shown in Table 3 and Table 4 for summary purposes) led to several questions that remain unanswered at present. First, it appears that auditory learning is somehow different during prenatal and postnatal development, and that these differences stem from the relative role that visual system development plays at different times in individual development. Chicks who are exposed to 10 min/hr of an individual bobwhite maternal call during the 24 hrs prior to hatching can successfully learn and remember this call for 24 hrs following hatching (Lickliter & Hellewell, 1992; Lickliter & Lewkowicz, 1995; Sleigh, Columbus, & Lickliter, 1996). Chicks who receive 10 min/hr exposure to the maternal call for the 24 hrs following hatching appear unable to learn this call (Columbus & Lickliter, 1997). The questions remains as to whether it is the timing of presentation of auditory information that is influential in determining chicks' auditory learning capacity, or whether the relative status of visual system development and experience during prenatal and postnatal development affects chicks' ability to learn auditory information. Finally, what exactly is

the nature of the relationship between prenatal and postnatal learning, and how does the organism's experiential history affect chicks' emerging learning capacity?

At this point, these questions remained unanswered, as most previous studies of auditory learning in precocial avian infants have simply focused on prenatal auditory learning capacity (Gottlieb, Tomlinson, & Radell, 1989; Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992; Sleigh, Columbus, & Lickliter, 1996). What remained to be explored is how visual experience presented at differing times in prenatal and postnatal development might differentially affect auditory learning ability during these developmental stages. This dissertation project was designed to answer these questions, by unpacking the role that visual experience plays during prenatal and postnatal development in bobwhite chicks' ability to learn auditory information.

IV. PURPOSE OF THE PRESENT STUDY

Regarding the specific studies that have been outlined thus far, what has been studied most often is how sensory stimulation provided to developing organisms affects their perceptual learning capacity. However, it is possible that the apparent negative effects of concurrent prenatal stimulation may be only transient. It might also be the case that patterns of learning during prenatal development are different from those present in postnatal development, and that these differences result from organismic changes in perceptual system functioning that occur in the shift from prenatal to postnatal life.

In this light, the present project was conducted to examine more closely how auditory learning capacity is affected by organismic characteristics such as the interrelationship between the developing auditory and visual systems in late prenatal/early postnatal development. Thus, this study was designed to provide answers to several specific problems that remained unanswered from previous examinations of early learning capacity in precocial avian embryos and infants. Specifically, this study attempted to provide answers to the following questions:

1. Are patterns of auditory learning during prenatal development different from those present during early postnatal development?
2. Does visual system experience during postnatal development cause forgetting of auditory information learned prenatally, and interfere with postnatal auditory learning?
3. What is the nature of the relationship between prenatal and postnatal learning and the role of experience in shaping this relationship?

V. HYPOTHESES AND PREDICTIONS

As we have seen, early learning capacity in developing organisms is necessarily constrained by the sensory systems of those developing organisms, providing structure and order to the developmental process. What previous studies have focused on is how types, amounts, and timing of stimulation provided to the various sensory systems affects what information is learned.

These initial studies suggest that interference from incoming stimulation to the later-developing visual system may disrupt the earlier-developing auditory system's

ability to process auditory information in the first two days following hatching. However, it is also possible that there is some fundamental change in organismic organization that occurs following hatching because the visual system becomes functional and stimulation to this modality interferes with the earlier-developing auditory system. This would indicate that the timing of auditory stimulation might affect chicks' ability to learn this information. In other words, it might be easier for chicks to learn auditory information during prenatal development, when their auditory systems normally become functional, than during postnatal development, when the visual system typically becomes functional and begins to compete with the auditory system. When viewed in light of previous studies of prenatal auditory learning in bobwhite quail chicks, it seems likely that unusually early visual stimulation provided during prenatal development interferes with chicks' ability to learn auditory information during the prenatal period (see Gottlieb, Tomlinson, & Radell for similar findings with duckling embryos). It also seems likely that delaying visual system development following hatching allows chicks to more easily remember auditory information (Lickliter & Hellewell, 1992). The current project was designed to examine these two related possibilities.

In summary, the current project was conducted to examine bobwhite quail chicks' early learning capacity in light of the sequential onset of sensory system functioning, and Turkewitz and Kenny's (1982) theory of competition within and between developing sensory systems. I examined how bobwhite quail chicks' auditory and visual experience throughout prenatal and postnatal development influenced their ability to learn an individual bobwhite quail maternal call in the periods prior to and following hatching. Specifically, the current project was designed to assess 1) whether unusually early visual experience interferes with the ability to learn auditory information during early prenatal and postnatal development and 2) whether normal or delayed visual experience affects auditory learning in the period prior to and following hatching.

Hypothesis 1:

It was hypothesized that bobwhite quail chicks who are socially reared in lighted conditions following hatching can demonstrate postnatal auditory learning by the first 72 hrs following hatching as a result of receiving regular exposure to a particular bobwhite maternal call (Call A), similarly to chicks in previous studies (Columbus & Lickliter, 1997). (Experiment 1A).

Hypothesis 2:

As seen in earlier studies, it was hypothesized that chicks receiving attenuated postnatal visual experience and regular postnatal exposure to a particular bobwhite maternal call (Call A) would demonstrate a similar postnatal ability to learn that maternal call after 24 hrs of exposure to that call (Experiment 1B).

Hypothesis 3:

It was expected that neither the prenatal egg-opening procedure nor unusually early prenatal visual stimulation would affect bobwhite quail chicks' preference for two individual variants of the bobwhite maternal assembly call (Call A or Call B), (Experiment 2).

Hypothesis 4:

According to Turkewitz and Kenny's (1982) sensory system competition theory and Radell and Gottlieb's (1992) developmental intersensory interference hypothesis, earlier-than-normal sensory stimulation from a later-developing sensory system potentially interferes with normal development of an earlier-developing sensory system. Therefore, it was hypothesized that prenatal visual experience would affect postnatal auditory learning, because the addition of earlier-than-normal visual experience would begin this system's functioning earlier in development. Specifically, the following three hypotheses were made:

- 3a) Beginning visual system experience earlier than normal (i.e., during prenatal development) should interfere with postnatal auditory learning, even when chicks are postnatally reared in light-attenuated conditions (Experiment 3C).
- 3b) Providing chicks with prenatal visual experience in addition to rearing chicks in normal, lighted conditions postnatally should lead to even greater deficits in auditory learning capacity as compared to chicks in Columbus and Lickliter (1997) and Experiment 1B (Experiment 3A).
- 3c) The prenatal egg-opening procedure and darkened prenatal conditions, followed by postnatal light-attenuated rearing conditions should lead to similar patterns of learning as seen in Columbus and Lickliter (1997), because visual experience will not be present to interfere with auditory learning (Experiment 3B).

Hypothesis 5:

Based on previous results suggesting that prenatal auditory learning differs from postnatal auditory learning (i.e., Lickliter & Hellewell, 1992), it was hypothesized that prenatal visual experience would not interfere with prenatal auditory learning, as long as the visual and auditory stimulation are presented nonconcurrently. The following specific hypotheses were made about prenatal learning and postnatal memory:

- 4a) Postnatal visual experience should interfere with processing of auditory information presented prenatally, which leads chicks to forget the information during postnatal development. In other words, continued stimulation to the visual system during postnatal development should potentially lead to deficits in chicks' ability to remember the call they heard during prenatal development (Experiment 4A).
- 4b) Attenuating postnatal visual experience should result in chicks' demonstrating the ability to remember auditory information they learned prenatally. In other words, postnatal visual attenuation may reduce intersensory interference and lead to chicks' successful remembrance of the call they heard during prenatal development (Experiment 4B).
- 4c) Finally, chicks who experience both prenatal and postnatal light-attenuated conditions should be able to learn and remember maternal auditory stimulation into later ages than chicks who are reared in lighted conditions (Experiment 4C).

General Method

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

Subjects

Subjects were 721 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 three or more different batches (weeks) of eggs. As a result of their incubator rearing, the only sounds to which the hatchlings were exposed 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 was illuminated by a 100-W brooder lamp, suspended above the plastic rearing tubs, which maintained an ambient air temperature of approximately 30°C. Food and water was continuously available throughout the duration of each experiment.

Egg Opening Procedure

To ensure that embryos were able to hear and see augmented prenatal auditory and visual stimulation, during the second half of the 21st day of incubation, the shell and inner-shell membrane over the air space of the egg of each subject was removed. The embryo's bill usually penetrates the air space early on Day 21, and it is at this time that the embryo begins to respire and vocalize (Freeman & Vince, 1974). Therefore, exposing the embryo's head during this time does not interfere with incubation, postural orientation, species-typical perceptual behavior, or survivability (Banker & Lickliter, 1993; Heaton & Galleher, 1981; Lickliter, 1990a; Sleigh & Lickliter, 1997). This procedure produces no bleeding and requires about 1 minute per egg. Following removal of part of the shell, opened eggs were placed in a Hovi-bator portable incubator for the last 24-36 hr of incubation. This incubator was equipped with a Plexiglass top, which allowed for stimulation of the embryos within. Temperature and humidity were maintained as during incubation, and as a result, experimental and control embryos did not differ in their developmental age at hatching.

Testing

Testing was conducted at 24, 48, 72, or 96 hrs (+/- 3 hr) of age following hatching. 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 were lined with foam to attenuate echoes, and the floor was painted flat black. Two rectangular approach areas (32 X 15 cm) were demarcated on opposite sides of the arena by green strips painted on the floor. These approach areas made up less than 10% of the total area of the arena. A midrange dome-radiator speaker was positioned behind the curtain in each of these two approach areas, equidistant from the point at which each chick was placed in the apparatus. Each speaker was 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 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 chick remained in an approach area during the 5 min test. When, over the course of the 5 min trial, 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 chick did not enter either approach area or 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 (see Appendix A for sample test scoring sheet).

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 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 were 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.

Experiment 1A: Effects of Species-Typical Postnatal Visual Experience on Auditory Learning

Research has demonstrated that bobwhite embryos can discriminate and learn an individual species-specific bobwhite maternal call during the prenatal period (Lickliter & Hellewell, 1992; Lickliter & Lewkowicz, 1995; Sleight, Columbus, & Lickliter, 1996). Results from Columbus and Lickliter (1997) also show that chicks can learn an individual maternal call (Call B) during the period following hatching. Chicks reared in lighted conditions require 72 hrs to learn an individual bobwhite maternal call, but chicks reared in light-attenuated conditions can learn Call B as early as 24 hrs following hatching. Taken together, these findings suggest that postnatal auditory learning appears to occur more easily when sensory stimulation from the visual modality is attenuated or absent during the postnatal period.

Interestingly, in these earlier studies embryos and hatchlings were exposed to the particular individual maternal Call B during early development. In light of the fact that learning typically occurs within an ecological niche with specific (but varying) stimulation, it would be useful to examine chicks' ability to learn a different maternal call following exposure to that call. The current experiment was designed to explore this possibility. Following the procedures used in Columbus and Lickliter (1997), chicks were socially reared in lighted conditions and exposed to a different individual maternal call (Call A) during the period following hatching.

Method

Subjects were 40 bobwhite quail chicks, drawn from four separate hatches to control for possible between-batch variation in subjects' behavior. 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, to mimic naturally occurring brood conditions (Stokes, 1967). Subjects received exposure to 10 min/hr of a recorded individual bobwhite maternal call, Call A, from hatching until testing. The call was broadcast to hatchlings through a Marantz Model PMD 221 cassette tape recorder and was presented at a peak intensity of 65 dB, as measured by a Bruel and Kjaer Model 2232 sound-level meter. All of the normally occurring acoustic components of the maternal vocalization were present and unaltered (see Heaton, Miller, & Goodwin, 1978 for acoustical details.) Food and water was continuously available to subjects throughout the experiment.

Previous studies have demonstrated that light-reared chicks who receive exposure to an individual maternal call (Call B) do not show a robust preference for that call until 72 hrs following hatching (Columbus & Lickliter, 1997). Therefore, chicks in this experiment were only tested at 72 (n = 20) and 96 hrs (n = 20) following hatching. Chicks were placed in the testing arena and given a simultaneous choice test between the familiar bobwhite maternal Call A and the unfamiliar bobwhite maternal Call B. Chicks were tested singly, and choice, latency, and duration of response were scored as described in the General Methods section.

Results and Discussion

Results for this experiment are shown in Tables 5 and 6. As expected, chicks socially reared in lighted conditions and exposed to 10 min/hr of bobwhite maternal Call

A following hatching demonstrated a significant preference for the familiar Call A at 72 hr , $\chi^2 (2) = 30.33$, $p < .001$, and 96 hr $\chi^2 (2) = 32.32$, $p < .001$, following hatching. Analyses of latency and duration scores supported these results, with chicks showing significantly shorter latencies and longer durations in their responses to the familiar Call A over the unfamiliar Call B at both 72 hr ($z = 3.72$ for latency, $z = 3.68$ for duration, $p < .001$ in both cases), and 96 hr ($z = 3.54$ for latency, $z = 3.82$ for duration, $p < .001$ in both cases).

These findings support and extend results found in Columbus and Lickliter (1997). In that study, socially reared chicks who received exposure to 10 min/hr of bobwhite maternal Call B following hatching showed strong preferences for that familiar call at 72 and 96 hrs of age. Chicks in the present experiment who received a similar sensory experience of 10 min/hr of maternal auditory stimulation during postnatal lighted conditions also demonstrated strong preferences for the familiar call to which they were exposed. Importantly, the results from this experiment show that bobwhite quail chicks show equivalent ability to learn either bobwhite maternal Call A or Call B. In fact, chicks in this experiment show similar magnitudes of preference as chicks in Columbus and Lickliter (1997) (see tables 3 and 4). These findings suggest that whichever individual maternal call chicks experience following hatching determines their pattern of auditory preference for that specific type of maternal stimulation. Importantly, this finding supports an ecological view of learning, as the ability to learn a specific maternal call would provide an important survival advantage for the young hatchling.

Given the similarity between findings in this experiment and results from the previous studies (i.e., Columbus & Lickliter, 1997), we hypothesized that chicks reared in postnatal light-attenuated conditions and exposed to 10 min/hr of Call A would show similar patterns of learning as chicks reared with Call B. The next experiment was designed to test this possibility.

Experiment 1B: Effects of Attenuated Postnatal Visual Experience on Auditory Learning

Previous research has demonstrated that chicks who are socially reared in lighted conditions, and are exposed to 10 min/hr of an individual maternal call (Call B), reliably demonstrate a significant preference for this call over an unfamiliar Call A by 72 hrs following hatching. On the other hand, chicks who are reared in light-attenuated conditions and are exposed to 10 min/hr of Call B prefer that familiar call as early as 24 hrs following hatching (Columbus & Lickliter, 1997). When viewed in light of interactions between the auditory and visual systems that occur in normal development, it seems likely that decreasing input to the visual modality during the period following hatching (by rearing them in light-attenuated conditions) would allow chicks to learn an individual maternal call more quickly than chicks who are reared in lighted conditions. The next experiment was designed to test this possibility, and thus served as an extension and replication of the results in Columbus and Lickliter (1997), in which chicks reared with Call B in light-attenuated conditions successfully learned that call within 24 hr following hatching.

Method

Subjects were 83 bobwhite quail chicks, drawn from seven separate hatches. Following hatching, chicks were reared in groups of 10-14 conspecifics and placed in a darkened portable brooder from hatching until testing at 24, 48, 72, or 96 hrs ($n = 20$ in each group). 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. While we could 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.

In addition to being reared in light-attenuated conditions, chicks were exposed to 10 min/hr of an individual bobwhite maternal call, Call A, from hatching until testing. The calls were broadcast through a Marantz Model PMD 221 cassette tape recorder at a peak intensity of 65 dB, as measured by a Bruel and Kjaer Model 2232 sound-level meter. Food and water were continuously available to the chicks throughout the experiment. Subjects were tested at 24, 48, 72, or 96 hrs following hatching. Immediately prior to testing, chicks were removed from the brooder and allowed to adjust their eyes to the light of the testing room for a period of 1-2 minutes, as in previous studies (Columbus & Lickliter, 1997, 1998; Lickliter, Lewkowicz, & Columbus, 1996).

Results and Discussion

Results from this experiment are shown in Tables 5 and 6. As expected, chicks socially reared in light-attenuated conditions and exposed to 10 min/hr of bobwhite maternal Call A demonstrated a significant preference for this familiar call at 24 hr, $\chi^2(2) = 6.4$, $p < .05$; 48 hr, $\chi^2(2) = 34.37$, $p < .001$; 72 hr, $\chi^2(2) = 18.11$, $p < .001$; and 96 hr $\chi^2(2) = 32.32$, $p < .001$. following hatching. Analysis of latency and duration scores supported these patterns of preference, with chicks showing significantly shorter latencies and longer durations in their responses to the familiar Call A over the unfamiliar Call B at all ages tested: 24 hr ($z = 2.65$ for latency, $p < .01$, $z = 2.24$ for duration, $p < .05$); 48 hr ($z = 3.75$ for latency, $z = 3.77$ for duration, $p < .001$ in both cases); 72 hr ($z = 2.33$ for latency, $p < .01$, $z = 3.68$ for duration, $p < .001$); and 96 hr ($z = 3.42$ for latency, $z = 3.82$ for duration, $p < .001$ in both cases).

As in Experiment 1A, these findings support and extend findings from Columbus and Lickliter (1997). Chicks reared in light-attenuated conditions and exposed to bobwhite maternal auditory stimulation (in this case, Call A) demonstrate the ability to learn that specific individual bobwhite maternal call at 24, 48, 72, and 96 hr following hatching, just as they do when postnatally exposed to 10 min/hr of Call B.

These results further support the idea that taking away one form of sensory stimulation (i.e., visual stimulation) during early postnatal development leads to more rapid learning of a maternal call, a form of auditory stimulation. In other words, decreasing one source of incoming sensory stimulation, in this case incoming visual information, appears to facilitate learning of another source of incoming sensory stimulation (i.e., auditory). Importantly, these results support Turkewitz and Kenny's (1982) sensory system interference hypothesis, in that limitations on visual system experience (a later-developing sensory system) enable chicks to process and learn auditory information (from an earlier-developing sensory system).

Taken together with results from Columbus and Lickliter (1997), the results from these first two experiments 1A and 1B raise several questions that remain unanswered at present. If interference from incoming visual stimulation causes slower learning of auditory information, what happens when the developing visual system begins to function even earlier in development, such as during the prenatal period? Will auditory learning deficits still occur? Can the effects of visual experience during prenatal development be attenuated by light-attenuated experience during postnatal development? The next experiments were designed to test how prenatal sensory experience works in conjunction with postnatal sensory experiences in molding auditory learning patterns.

Experiment 2: Effects of Prenatal Egg-Opening Procedure on Naïve Postnatal Auditory Preference Between Call A and Call B

Previous studies with bobwhite quail have focused on prenatal determinants of early learning capacity (Lickliter & Hellewell, 1992; Lickliter & Lewkowicz, 1995; Sleigh, Columbus, & Lickliter, 1996). Specifically, these studies have demonstrated that embryos who are socially reared with other chicks (Lickliter & Hellewell, 1992), socially reared with visual stimulation (Lickliter & Lewkowicz, 1995), or socially reared with exposure to bobwhite hatchling contentment calls (Sleigh, Columbus, & Lickliter, 1996) reliably show a preference for the familiar bobwhite maternal call over an unfamiliar call. On the other hand, chicks who are reared in physical isolation (Lickliter & Lewkowicz, 1995) or are reared with exposure to hatchling distress calls (Sleigh, Columbus, & Lickliter, 1996) fail to learn an individual bobwhite maternal call.

Taken together, results from these related studies suggest that prenatal auditory learning in bobwhite quail embryos can be influenced by social experience, as well as by the type and timing of auditory sensory stimulation provided during the prenatal period. To date, however, few studies have examined how subjects' early learning capacity is shaped by their sensory stimulation histories during early postnatal development (but see Columbus & Lickliter, 1997). If factors such as social experience, type of stimulation, and timing of stimulation shape early learning capacity during the prenatal period, it seems likely that these factors will also affect learning during postnatal development as well. Since previous research has demonstrated that the timing of stimulation can affect early perceptual development (Banker & Lickliter, 1993; Columbus & Lickliter, 1998; Lickliter, 1993), altering chicks' sensory stimulation experiences during the perinatal period may differentially affect their ability to learn an individual bobwhite maternal call. Experiments 3A, 3B, and 3C were designed to test this possibility. However, first it was necessary to control for possible naïve preferences for individual bobwhite maternal calls A and B.

Experiment 2 was designed to examine whether the prenatal egg-opening procedure affects embryos' subsequent preference for two individual variants of a bobwhite maternal call (Call A and Call B). It is possible that providing embryos with prenatal visual stimulation affects chicks' naïve preference for Call A and Call B. Thus, this current experiment served as a control for Experiments 3A, 3B, and 3C, which examined whether providing embryos with unusually early prenatal visual stimulation affected subsequent auditory preference.

Method

Subjects were 86 bobwhite hatchlings, drawn from eight separate hatches to control for possible between-batch variation in subjects' behavior. On day 21 of incubation, subjects underwent the egg-opening procedure as described in General Methods. Subjects were then incubated in groups of 10-14 same-aged embryos and exposed to 10 min/hr of patterned visual stimulation by means of a 15-W light pulsed at 3 cycles per second (maximum flash energy = 4 W s) for the 24 hrs immediately prior to hatching. Thus, chicks received a total of 240 minutes of prenatal patterned visual stimulation. This temporally patterned light was located immediately above (4 cm) the plexiglas top of the incubator. Care was taken to ensure that the presence of the light did not alter the ambient air temperature or relative humidity of the incubator.

Chicks received 10 min/hr of prenatal visual stimulation until hatching, at which point they were transferred to tubs and socially reared in lighted conditions until testing at 24, 48, 72, or 96 hr following hatching. Chicks were tested in a simultaneous-choice test between Call A and Call B as described in earlier experiments. Chicks received no exposure to either bobwhite maternal call A or B at any point in development, and thus were maternally naïve at testing.

Results and Discussion

Results for this experiment are shown in Tables 7 and 8. As can be seen in these tables, chicks who received 10 min/hr of prenatal visual stimulation but no prenatal or postnatal exposure to maternal auditory stimulation failed to show a significant preference for Call A or Call B at any age tested: 24 hr ($\chi^2(2) = 4.0, p > .05$), 48 hr ($\chi^2(2) = 0.12, p > .05$), 72 hr ($\chi^2(2) = 0, p > .05$), and 96 hr ($\chi^2(2) = 1.0, p > .05$). Analysis of latency and duration scores supported these patterns of preference, with chicks showing no differences in latencies or durations in their responses to either call at 24 hr ($z = 0.11$ for latency, $z = 0.04$ for duration, $p > .05$ in both cases), 48 hr ($z = 1.63$ for latency, $z = 0.36$ for duration, $p > .05$ in both cases), 72 hr ($z = 0.59$ for latency, $z = 0.02$ for duration, $p > .05$ in both cases), or 96 hr ($z = 0.41$ for latency, $z = 1.42$ for duration, $p > .05$ in both cases) following hatching.

Experiment 3A: Effects of Prenatal Visual Stimulation + Postnatal Auditory and Visual Experience on Auditory Learning

Previous research has demonstrated that bobwhite quail embryos exposed to 10 min/hr of patterned visual experience during the last 24-36 hr of incubation exhibit an accelerated pattern of species-typical perceptual responsiveness in the days following hatching (Lickliter, 1990a, 1990b, 1994). Chicks that receive moderate amounts of unusually early visual stimulation respond to species-specific maternal auditory and visual cues as early as 24 hrs following hatching (Lickliter, 1990b; 1994). These results contrast with unmanipulated chicks, who fail to respond to integrated maternal auditory-visual cues until 72 hrs following hatching (Lickliter, 1994; Lickliter & Virkar, 1989).

Although 10 min/hr of prenatal visual stimulation accelerates auditory-visual functioning in bobwhite chicks, substantially augmented prenatal visual stimulation delays auditory-visual functioning. Specifically, Sleigh and Lickliter (1995) found that

providing bobwhite embryos with 40 min/hr of prenatal visual stimulation interfered with chicks' species-typical patterns of intersensory responsiveness, as well as their ability to learn a specific bobwhite maternal call. These findings suggest that this substantially augmented amount of prenatal visual stimulation falls outside some optimal range of stimulation necessary for species-typical development and learning capacity (Sleigh & Lickliter, 1995).

These studies have revealed that visual responsiveness is accelerated in chicks who receive moderate amounts of prenatal visual stimulation (Lickliter 1990a, 1990b, 1994), but chicks' auditory responsiveness is altered by this visual experience. Chicks who receive 10 min/hr of prenatal visual stimulation do not prefer species-specific auditory cues at 24 and 48 hrs following hatching (Lickliter, 1990a), in contrast with unmanipulated control chicks (Lickliter & Virkar, 1989).

In sum, results from these previous studies have demonstrated that early visual experience decreases auditory responsiveness and accelerates visual functioning in the days following hatching (Lickliter 1990a, 1990b, 1994), as long as this visual stimulation falls within some optimal range of sensory stimulation (Sleigh & Lickliter, 1995). It is possible then, that since prenatal visual stimulation affects postnatal patterns of responsiveness to maternal cues, this form of stimulation may also affect postnatal auditory preferences for individual bobwhite maternal calls.

Results of Experiment 1A showed that bobwhite chicks who are socially reared in lighted conditions and exposed to 10 min/hr of a specific bobwhite maternal call postnatally, demonstrate the ability to learn that call by 72 hrs following hatching. However, when chicks are reared in light-attenuated conditions and exposed to 10 min/hr of a specific bobwhite maternal call following hatching, they demonstrate the ability to learn this call as early as 24 hrs following hatching (Experiment 1B). These findings from Experiments 1A and 1B suggest that postnatal visual experience normally present in species-typical rearing conditions may potentially interfere with chicks' ability to learn auditory information. Since the visual system begins to receive input immediately following hatching (the presence of the egg prevents this stimulation during prenatal development), subsequent visual system development may compete with the earlier-developing auditory system, leading to deficits in auditory learning ability in newly hatched chicks.

The following experiment was conducted to assess whether prenatal visual system experience interferes with postnatal auditory learning. Chicks received 10 min/hr (total = 240 min) prenatal visual stimulation, thus beginning visual system development at an earlier point in development than for chicks in Experiments 1A and 1B. Following hatching, chicks were reared in lighted conditions and were provided with exposure to either Call A or Call B. If visual system experience interferes or competes with the already developing auditory system, then chicks with even earlier-than-normal visual system experience (and thus, more visual experience) should fail to learn the maternal call to which they are exposed by 72 hrs of age (when chicks in Experiment 1A successfully demonstrate auditory learning).

Method

Subjects were 82 bobwhite embryos and hatchlings, drawn from five separate hatches to control for possible between-batch variation in subjects' behavior. On day 21

of incubation, subjects underwent the egg-opening procedure as described in General Methods. Subjects were then incubated in groups of 10-14 same-aged embryos and were exposed to 10 min/hr of patterned visual stimulation by means of a 15-W light pulsed at 3 cycles per second (maximum flash energy = 4 W s) for the 24 hrs immediately prior to hatching. Thus, chicks received a total of 240 minutes of prenatal patterned visual stimulation. This temporally patterned light was located immediately above (4 cm) the plexiglas top of the incubator. Care was taken to ensure that the presence of the light did not alter the ambient air temperature or relative humidity of the incubator.

Chicks received 10 min/hr of prenatal visual stimulation until hatching, at which point they were transferred to large plastic tubs and reared in conditions similar to those in Experiment 1A. Specifically, chicks were socially reared in lighted conditions in groups of 10-14 conspecifics, to mimic naturally occurring brood conditions (Stokes, 1967). In addition, subjects received postnatal exposure to 10 min/hr of a recorded individual bobwhite maternal call from hatching until testing at 24, 48, 72, or 96 hrs ($n = 20$ in each group). In each group, 10 chicks received exposure to bobwhite maternal Call A, while the other 10 chicks received exposure to bobwhite maternal Call B, to counterbalance for possible bias in chicks' ability to learn either call. The calls were broadcast to hatchlings through a Marantz Model PMD 221 cassette tape recorder and were presented at a peak intensity of 65 dB, as measured by a Bruel and Kjaer Model 2232 sound-level meter. All of the normally occurring acoustic components of the maternal vocalizations were present and unaltered. Food and water were continuously available to subjects throughout the experiment. Testing occurred at 24, 48, 72, or 96 hrs following hatching in a simultaneous choice test between Call A and Call B. Chicks were tested singly, and choice, latency, and duration of response was scored as described in General Methods.

Results and Discussion

Results for this experiment are shown in Tables 9 and 10. Surprisingly, and contrary to hypothesized results, chicks who received 10 min/hr of prenatal visual stimulation and 10 min/hr of postnatal maternal auditory stimulation in lighted conditions successfully learned the familiar call to which they had been exposed (either Call A or Call B) at 24 hr, $\chi^2(2) = 14.63$, $p < .001$, 48 hr, $\chi^2(2) = 6.42$, $p < .05$, 72 hr, $\chi^2(2) = 40.0$, $p < .001$, and 96 hr $\chi^2(2) = 30.33$, $p < .001$, at all ages tested. Analysis of latency and duration scores further supported these observed patterns of auditory learning and preference, with chicks showing shorter latencies and longer durations for the familiar calls they had heard in postnatal lighted conditions at all ages tested: 24 hr ($z = 2.45$ for latency, $p < .01$, $z = 2.29$ for duration, $p < .05$); 48 hr ($z = 2.74$ for latency, $p < .01$, $z = 1.81$ for duration, $p < .05$); 72 hr ($z = 3.81$ for latency, $z = 3.92$ for duration, $p < .001$ in both cases); and 96 hr ($z = 3.5$ for latency, $z = 3.63$ for duration, $p < .001$ in both cases).

These patterns of preference are particularly strong, in that most individual preference scores and latency and duration scores were significant at $p < .01$ or higher. More importantly, they stand contrary to what was expected based on previous research. It was expected that chicks receiving prenatal visual system stimulation by means of patterned light would learn at a slower rate, resulting from the augmented visual stimulation they received during prenatal development. Specifically, chicks should have failed to learn the call by ages when chicks not receiving prenatal visual experience

normally learn the bobwhite maternal call (i.e., by 72 hr as in Experiment 1A). Instead, chicks who received 10 min/hr of augmented prenatal visual stimulation, followed by visual stimulation postnatally paired with 10 min/hr of maternal auditory information learned the call by the same age that chicks who are dark-reared prenatally and dark-reared postnatally learn the bobwhite maternal call, as seen in Experiment 1B and Columbus and Lickliter (1997).

At first glance these findings do not appear to support previous research examining sensory system competition and interference (i.e., Gottlieb, Tomlinson, & Radell, 1989; Kenny & Turkewitz, 1986; Lickliter & Lewkowitz, 1995). Based on this work, earlier-than-normal visual system experience should interfere with auditory learning ability, and chicks receiving this visual stimulation should demonstrate delays in auditory learning as a result of competition between these two sensory modalities for cognitive resources. This, however, does not appear to be the case in the present experiment. In fact, prenatal visual experience appears to facilitate auditory learning in bobwhite quail hatchlings, rather than slowing this process down.

However, this finding is consistent with previous studies examining prenatal visual experience and postnatal functioning (Lickliter, 1990; Lickliter & Stoumbos, 1991; Radell & Gottlieb, 1992; Sleigh & Lickliter, 1996). In these studies, prenatal auditory or visual experiences that fall within some optimal range appear to maintain or facilitate normal patterns of perceptual functioning. Specifically, Lickliter and Stoumbos (1991) found that moderately enhanced amounts of embryonic vocalizations that typically occur in the late prenatal environment serve to facilitate postnatal visual functioning. Additionally, Lickliter (1990a, b) found that 10 min/hr of prenatal visual stimulation accelerates postnatal intersensory responsiveness, and Sleigh and Lickliter (1996) demonstrated that chicks exposed to 10 min/hr of contentment calls show accelerated visual response patterns. In light of these earlier studies, it appears that in the present experiment, 10 min/hr of prenatal visual experience was an optimal amount of stimulation to facilitate chicks' postnatal auditory learning ability. What is interesting about this finding is that in this case, prenatal visual stimulation (from a later-developing sensory system) facilitated learning of postnatal auditory information (from an earlier-developing sensory system).

One possible explanation is that chicks who do not receive prenatal visual experience do not have a chance to adjust to visual sensory stimulation prenatally. When they are then exposed to both visual and maternal auditory information following hatching, it may take longer for chicks to adjust to two differing forms of concurrent sensory stimulation (i.e., auditory and visual stimulation) that are occurring simultaneously during postnatal development. In other words, when the prenatal and postnatal sensory environments present a "mismatch," it may fuel competition between the visual and auditory sensory systems during early postnatal development. However, a "match" between patterns of prenatal and postnatal sensory stimulation may facilitate perceptual learning and development by "spreading out" the adjustment period of integrating sensory information from two differing sensory modalities over the course of prenatal and postnatal development. This explanation has been supported by earlier studies of mismatches between prenatal and postnatal stimulation histories (McBride & Lickliter, 1995).

Experiment 3B: Effects of Prenatal Light-Attenuation and Postnatal Light-Attenuation + Maternal Auditory Stimulation on Postnatal Auditory Learning

The previous experiment was designed to assess whether prenatal visual experience, in addition to normally-available postnatal visual experience, interferes with and/or delays typical patterns of postnatal auditory learning in bobwhite quail chicks. The results from that experiment suggest that, rather than delaying postnatal auditory learning, moderate amounts of prenatal visual experience may actually facilitate postnatal learning by allowing embryos to “adjust” to this new form of sensory stimulation prior to hatching. These findings would suggest that, in light of Turkewitz and Kenny’s (1982) sensory limitations hypothesis, competition between sequentially developing sensory systems could be ameliorated by providing moderate amounts of a later developing sensory system during earlier periods in development, thus diffusing the effects of the new type of sensory stimulation.

Importantly for the present experiment, these findings would suggest that a mismatch between prenatal and postnatal visual stimulation should be detrimental postnatal learning ability. This raises the interesting possibility that providing matching prenatal and postnatal sensory experiences might facilitate postnatal auditory learning, whether these experiences consisted of visual stimulation or the absence of visual stimulation. For example, bobwhite embryos typically receive little visual sensory stimulation during prenatal development, as the egg prevents light from entering the prenatal environment. Postnatally, however, chicks immediately receive ongoing visual stimulation. If we take away this normal source of visual stimulation, it seems likely that chicks could learn auditory information just as quickly as they did in Experiments 1B and 3A, and Columbus and Lickliter (1997).

Previous studies have demonstrated that, in some cases, the same species-typical developmental outcomes can result from two or more different preceding types of experience. Gottlieb (1991) has suggested that there are many instances of how multiple pathways in development lead to similar outcomes. For example, Miller, Hicinbothom, & Blaich (1990) recently examined the effects that different developmental experiences have on similar developmental outcomes. Previous studies found that prenatal auditory experience is necessary for postnatal freezing responses to the duckling maternal alarm call. However, Miller and colleagues found that socially reared, devocalized mallard ducklings reliably demonstrate the freezing response, even though they have been denied prenatal auditory experience. These results suggest that there are potentially multiple pathways to similar outcomes in behavioral development.

Research with bobwhite quail chicks have provided similar results to those found by Miller, Hicinbothom, & Blaich (1990). For example, Banker and Lickliter (1993) examined the relative impact of early and delayed visual experience on intersensory development in bobwhite quail embryos and hatchlings. In this study, chicks that were denied postnatal visual experience (by means of eye-patches) from hatching until testing sustained an auditory preference for the bobwhite maternal call into later stages of postnatal development than control chicks (Banker & Lickliter, 1993; Lickliter & Virkar, 1989). These results suggest that the early pattern of auditory dominance seen in control chicks extends to subjects who fail to receive postnatal visual experience. Chicks in a second experiment in this study were provided with 10 min/hr prenatal visual stimulation,

but were denied postnatal visual stimulation following hatching. Results revealed that chicks in this condition showed a significant preference for the bobwhite maternal call at 24 and 48 hrs following hatching, but by 72 hrs, required both auditory and visual cues to direct their filial responsiveness (Banker & Lickliter, 1993). Thus, chicks showed patterns of auditory responsiveness similar to that of unmanipulated control chicks (Lickliter & Virkar, 1989), indicating that the effects of augmented prenatal visual stimulation were “cancelled out” by the attenuated postnatal visual stimulation (Banker & Lickliter, 1993).

Recently, Columbus and Lickliter (1998) demonstrated that timing of postnatal visual stimulation has a profound effect on subsequent auditory-visual responsiveness in bobwhite chicks. Chicks in this study were provided with one of two postnatal visual conditions following hatching. Chicks in one group were reared with attenuated postnatal visual experience in a darkened portable incubator during the first 36 hrs following hatching, and were then transferred to normal, lighted conditions for the next 36 hrs prior to testing. Chicks in a second group were reared in normal, lighted conditions for the first 36 hrs following hatching, and were then transferred to a darkened, portable incubator for the last 36 hrs prior to testing at 72 hrs. Chicks who received early light-attenuated experience demonstrated altered postnatal visual responsiveness at testing. Chicks who received later light-attenuated experience demonstrated species-typical, or normal, patterns of visual responsiveness at 72 hrs following hatching (Columbus & Lickliter, 1998). These findings indicate that the timing of visual stimulation can affect subsequent postnatal perceptual responsiveness.

In a previous learning study, Lickliter and Hellewell (1992) found that chicks who were exposed to 10 min/hr of an individual bobwhite maternal call in the 24 hrs following hatching were unable to learn this call, in that they did not prefer the familiar call at 48 and 72 hrs following hatching. However, if chicks were reared in physical isolation following hatching and were exposed to 10 min/hr of the maternal call demonstrated successful auditory learning at 48 hrs following hatching. In light of the present experiment, these results suggest that there are potentially multiple pathways to achieving similar learning outcomes in early development. Lickliter and Hellewell (1992) utilized physical isolation to attenuate postnatal sensory experience, but chicks in the present study were exposed to attenuated postnatal visual experience.

Method

Subjects were 86 bobwhite quail embryos and hatchlings, drawn from four separate hatches to control for possible between-batch variation in subjects' behavior. Chicks in this experiment received the same experimental manipulations as chicks in Experiment 3A, except they were reared in light-attenuated conditions prior to and following hatching. In other words, on day 21 of incubation, embryos underwent the egg-opening procedure as described in General Methods. Subjects were then socially incubated in darkened conditions until hatching.

Following hatching, chicks were reared in groups of 10-14 conspecifics and placed in a darkened portable brooder from hatching until testing at 24, 48, 72, or 96 hrs ($n = 20$ in each group). 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.

In addition to being reared in light-attenuated conditions throughout prenatal and early postnatal development, chicks were postnatally exposed to 10 min/hr of an individual bobwhite maternal call (either Call A or Call B) from hatching until testing. The calls were broadcast through a Marantz Model PMD 221 cassette tape recorder placed on top of the portable brooder at a peak intensity of 65 dB, as measured by a Bruel and Kjaer Model 2232 sound-level meter. Food and water were continuously available to the chicks throughout the experiment. Subjects were tested at 24, 48, 72, or 96 hrs following hatching in a simultaneous choice test between bobwhite maternal Call A and Call B. Immediately prior to testing, chicks were removed from the brooder and allowed to adjust their eyes to the light of the testing room for a period of 1-2 minutes, as in previous studies (Columbus & Lickliter, 1997, 1998; Lickliter, Lewkowicz, & Columbus, 1996).

Results and Discussion

Results for this experiment are shown in Tables 9 and 10. As can be seen in the tables, chicks reared in prenatal and postnatal light-attenuated conditions successfully learned the call to which they were exposed at 24 hr, $\chi^2(2) = 14.0$, $p < .001$; 48 hr, $\chi^2(2) = 11.2$, $p < .01$; 72 hr, $\chi^2(2) = 19.9$, $p < .001$; and 96 hr, $\chi^2(2) = 12.25$, $p < .01$. Analysis of latency and duration scores supported these patterns of individual preference, with chicks showing shorter latencies and durations in their responses to the familiar call over the unfamiliar call at 24 hr ($z = 2.66$ for latency, $z = 2.8$ for duration, $p < .01$ in both cases), 48 hr ($z = 2.95$ for latency, $z = 2.56$ for duration, $p < .01$ in both cases), 72 hr ($z = 3.62$ for latency, $z = 3.51$ for duration, $p < .001$ in both cases), and 96 hr ($z = 3.47$ for latency, $z = 3.16$ for duration, $p < .001$ in both cases).

These results are similar to those found in Experiment 3A, where chicks reared with prenatal and postnatal visual stimulation successfully learned a maternal call during postnatal development within 24 hr of hatching. As outlined above, chicks reared in the absence of prenatal and postnatal visual stimulation also successfully demonstrated auditory learning within the first 24 hr of postnatal development. In summary, chicks in these two experiments demonstrated the same patterns of auditory learning, despite having two very different types of sensory stimulation and learning environments.

Experiment 3C: Effects of Prenatal Visual Stimulation and Postnatal Auditory Experience + Attenuated Visual Experience on Auditory Learning

When viewed together, results from the previous two experiments support the notion that there are multiple developmental pathways to the same developmental outcome. They also provide preliminary support for the hypothesis that matching amounts, types or intensities of prenatal and postnatal sensory stimulation potentially diffuses competition between developing sensory systems and facilitates auditory learning. This raises the interesting possibility that imposing greater differences in amounts or types of early perinatal stimulation that provide a “mismatch” between prenatal and postnatal patterns of stimulation might lead to deficits in postnatal auditory learning. This experiment was designed to examine this possibility.

Method

Subjects were 84 bobwhite embryos and hatchlings, drawn from ten separate hatches to control for possible between-batch variation in subjects' behavior. On day 21 of incubation, subjects underwent the egg-opening procedure as described in General Methods. Subjects were incubated in groups of 10-14 same-aged embryos and were exposed to 10 min/hr of patterned visual stimulation by means of a 15-W light pulsed at 3 cycles per second (maximum flash energy = 4 W s) for the 24 hrs immediately prior to hatching. Thus, chicks received a total of 240 minutes of prenatal patterned visual stimulation. This temporally patterned light was located immediately above (4 cm) the plexiglas top of the incubator. Care was taken to ensure that the presence of the light did not alter the ambient air temperature or relative humidity of the incubator. Chicks received 10 min/hr of prenatal stimulation until hatching, at which point they were transferred to the darkened portable brooder and reared in light-attenuated conditions, as described in the previous experiment. In addition to being reared in light attenuated conditions, chicks also received postnatal exposure to 10 min/hr of bobwhite maternal Call A (n = 10) or Call B (n = 10) broadcast from tape players located on top of the brooders. Food and water were continuously available to the chicks throughout the experiment. Subjects were tested at either 24, 48, 72, or 96 hr following hatching using the simultaneous choice test between Call A and Call B, as in the previous experiments. Chicks were allowed to let their eyes adjust to the light of the testing room for a period of 1-2 minutes prior to testing.

Results and Discussion

Results are shown in tables 9 and 10. As can be seen in the tables, chicks reared in prenatal darkened and postnatal light-attenuated conditions failed to successfully learn the call at 24 hr ($\chi^2(2) = 5.47, p > .05$). In contrast, chicks successfully learned the call at 48 hr, ($\chi^2(2) = 12.1, p < .01$), 72 hr, ($\chi^2(2) = 29.2, p < .001$), and 96 hr, ($\chi^2(2) = 24.7, p < .001$). Analysis of latency and duration scores further supported these patterns of individual preference, with chicks showing no differences in latency and duration scores to either the unfamiliar or familiar calls at 24 hr ($z = 0.2$ for latency, $p > .01$, $z = 1.13$ for duration, $p > .01$). In contrast, chicks demonstrated shorter latencies and durations in their responses to the familiar over the unfamiliar call at 72 hr ($z = 3.66$ for latency, $z = 3.77$ for duration, $p < .001$ in both cases) and 96 hr ($z = 3.62$ for latency, $z = 3.68$ for duration, $p < .001$ in both cases). While chicks tested at 48 hr demonstrated no differences in their latency scores between the two maternal calls ($z = 1.44$ for latency, $p > .05$), their duration scores did support the individual preference patterns reported above ($z = 2.3$ for duration, $p < .05$).

These results support the hypothesis that mismatches in types of prenatal and postnatal visual stimulation can affect postnatal auditory learning ability. Chicks in the current experiment who received 24 hr of visual experience prenatally, at a time they would not normally experience this stimulation, showed delayed auditory learning during early postnatal development. In contrast, chicks who did not receive prenatal visual experience and were reared in light-attenuated conditions during postnatal development learn maternal auditory information by 24 hr following hatching (Columbus & Lickliter, 1997; Experiment 1B). However, chicks in the present experiment who received prenatal

visual stimulation failed to demonstrate a preference for their familiar individual maternal call until 48 hr following hatching, indicating a 24 hr delay in auditory learning capacity.

Together, results from Experiments 3A, 3B, and 3C support Turkewitz and Kenny's (1982) sensory system limitations hypothesis that competition between incoming sources of sensory stimulation from two separate sensory modalities can negatively affect species-typical developmental outcome. Their hypothesis holds that premature stimulation from a later-developing sensory system can lead to deficits in typical behavioral organization and development. This theory is supported by results found with chicks in Experiment 3C, who received prenatal visual experience prior to hatching, then showed auditory learning delays during the first 24 – 48 hr of postnatal development. It appears that 24 hr of premature (i.e., prenatal) visual experience is sufficient to delay postnatal auditory learning by at least 24 hr. In addition, results from Experiment 3A indicate that nonconcurrent premature visual experience may facilitate postnatal auditory learning when chicks are reared in lighted conditions, with chicks learning maternal auditory information as early as 24 hr following hatching. Finally, when the opportunity for visual experience is removed from the postnatal rearing environment, chicks also demonstrate auditory learning at 24 hr (Experiment 3B). These findings from Experiments 3A, 3B, and 3C thus indicate that prenatal experiences affect chicks' ability to learn auditory information during postnatal development. In particular, the results of Experiment 3C suggest that mismatches in type and amount of prenatal and postnatal sensory stimulation can delay auditory learning during early postnatal development. It is possible that even greater differences between the type of prenatal and type of postnatal stimulation could create more competition between chicks' developing sensory systems than when the overall amount of stimulation is "spread out" between prenatal and postnatal development.

These findings that prenatal experience affects postnatal auditory learning raised the interesting question of whether similar effects to those outlined above occurred in embryos' prenatal learning abilities. More specifically, if prenatal experience affects subsequent postnatal learning, it seemed likely that postnatal experience might also affect chicks' ability to remember information they had learned previously as embryos. The next experiments were designed to explore this possibility.

Experiment 4A: Effects of Prenatal Visual Stimulation + Auditory Experience, and Species-Typical Postnatal Visual Stimulation on Auditory Learning

Previous studies examining learning capacity in bobwhite chicks have found that prenatal visual experience can interfere with prenatal auditory learning. Lickliter and Hellewell (1992) found that embryos who were exposed to 10 min/hr of concurrent visual and auditory stimulation during the last day of incubation failed to learn an individual bobwhite maternal call. However, embryos who were exposed to nonconcurrent visual and auditory stimulation preferred the bobwhite maternal call to which they were exposed in subsequent postnatal tests.

Experiments 3A, 3B, and 3C were designed to examine how prenatal visual experience interferes with postnatal auditory learning. In contrast, Experiments 4A, 4B, and 4C served to examine (a) how prenatal visual experience potentially impacts prenatal

auditory learning, and (b) whether chicks' ability to remember this information is affected by their postnatal rearing environment. By way of review, it was hypothesized in Experiments 3A and 3C that earlier than normal visual system experience would interfere with postnatal patterns of auditory learning when chicks were reared in lighted conditions. It was also proposed that postnatal attenuation of visual experience might slow visual system development, which would enable chicks to successfully learn auditory information during the period following hatching, thus somewhat reversing the effects of prenatal visual experience (Experiment 3C).

Are patterns of perceptual learning during prenatal development different from those patterns during postnatal development? Results from Lickliter and Hellewell (1992) would suggest that this is indeed the case. In that study, bobwhite embryos who hear an individual bobwhite maternal call during the 24 hrs prior to hatching can learn and remember that call for 24 hrs following hatching, but no longer show a preference for that call by 48 hrs following hatching. In addition, chicks who are exposed to 10 min/hr of nonconcurrent prenatal visual stimulation and 10 min/hr of the bobwhite maternal call can learn that call and remember it for 24 hrs following hatching. Based on results from Experiment 1B, it appears that postnatal auditory learning is also compromised by concurrent postnatal visual experience. However, results from Lickliter and Hellewell (1992) suggest that prenatal auditory learning is not compromised by visual experience (as long as the visual experience is provided nonconcurrently). These findings would suggest that prenatal auditory learning is somehow different from postnatal auditory learning.

The current experiment served to partially replicate and extend the findings of Lickliter and Hellewell (1992), in which chicks' patterns of postnatal auditory preference were tested until chicks were 48 hrs old. What still remains unexplored is how chicks respond at later ages. For example, chicks in Experiment 1B successfully demonstrated auditory learning by 72 hrs following hatching, but not at 24 and 48 hrs. It is possible that chicks in Lickliter and Hellewell's (1992) study would have demonstrated a re-emergent demonstration of auditory learning ability had they been tested at ages later than 48 hrs. Thus, the current experiment examined the effects of prenatal visual stimulation and prenatal auditory experience on postnatal patterns of preference for the familiar maternal call at 24, 48, 72, and 96 hrs following hatching.

Method

Subjects were 80 bobwhite quail embryos and hatchlings, drawn from four separate hatches to control for possible between-batch variation in subjects' behavior. On day 21 of incubation, subjects underwent the egg-opening procedure as described in General Methods. Subjects were then be incubated in groups of 10-14 same-aged embryos and were exposed to 10 min/hr of patterned visual stimulation by means of a 15-W light pulsed at 3 cycles per second (maximum flash energy = 4 W s) for the 24 hrs immediately prior to hatching. Thus, chicks received a total of 240 minutes of prenatal patterned visual stimulation. This temporally patterned light was located immediately above (4 cm) the plexiglas top of the incubator.

In addition to the patterned visual stimulation, embryos also received nonconcurrent exposure to 10 min/hr of a recorded individual bobwhite maternal call for the 24 hrs immediately prior to hatching. Half the embryos (n = 40) received exposure to

Call A, while the other half ($n = 40$) heard Call B, to counterbalance for possible bias in chicks' ability to learn either call. The calls were broadcast to embryos through a Marantz Model PMD 221 cassette tape recorder and were presented at a peak intensity of 65 dB, as measured by a Bruel and Kjaer Model 2232 sound-level meter. In other words, embryos in this experiment received 10 min/hr of patterned visual stimulation, followed by 10 min/hr of the recorded bobwhite maternal call (Call A or Call B) each hour for the 24 hrs prior to hatching. Care was taken to ensure that the presence of the light and cassette tape recorder did not alter the ambient air temperature or relative humidity of the incubator.

Following hatching, chicks were socially reared in lighted conditions, in large plastic tubs in groups of 10-14 conspecifics. Chicks were tested at 24, 48, 72, or 96 hrs following hatching ($n = 20$ in each group) in a simultaneous choice test between bobwhite maternal Call A and Call B. Chicks were tested singly, and choice, latency, and duration of response were scored as described in General Methods.

Results and Discussion

Results are shown in Tables 11 and 12. As can be seen in the tables, chicks reared with nonconcurrent prenatal visual and auditory stimulation demonstrated a significant preference for the familiar call over the unfamiliar call at 24 hr ($\chi^2(2) = 7.6$, $p < .05$) and 48 hr ($\chi^2(2) = 9.1$, $p < .05$) following hatching. In contrast, chicks failed to demonstrate a significant preference for the familiar call at 72 hr ($\chi^2(2) = 4.0$, $p > .05$) and 96 hr ($\chi^2(2) = 3.0$, $p > .05$) of age. Analysis of latency and duration scores partially supported these patterns of individual preference. Chicks demonstrated no reliable difference in latency scores between the familiar and unfamiliar maternal calls at 24 hr ($z = 1.49$ for latency, $p > .05$) but did demonstrate shorter latencies for the familiar call at 48 hr ($z = 1.7$, $p < .05$). Chicks showed significantly longer duration scores for the familiar call at 24 hr ($z = 1.72$, $p < .05$) and 48 hr ($z = 1.7$, $p < .05$).

As expected, chicks demonstrated no differences in latency scores at 72 hr ($z = 1.46$, $p > .05$) and 96 hr ($z = 0.63$, $p > .05$). However, chicks at both 72 hr and 96 hr showed longer duration scores to the familiar call over the unfamiliar call ($z = 1.72$, $z = 2.07$ respectively, $p < .05$ in both cases). In other words, chicks tested at these ages did not indicate individual preference for one call over the other, and their latencies did not differ in response to these calls. However, they did spend more time near the familiar call than the unfamiliar call during the test situation at both 72 hr and 96 hr. One measure out of three does not indicate a strong pattern of preference, however, so these results will be interpreted in terms of the patterns of individual preference for the familiar versus unfamiliar calls.

The patterns of preference observed in this experiment suggest that chicks can learn a call they heard during prenatal development and remember this call until at least 48 hr following hatching. However, it appears that chicks forget this call by 72 hr following exposure. Importantly, the current results successfully replicate Lickliter and Hellewell (1992) at 24 hr, but not at 48 hr. In that study, chicks who received 24 hr of nonconcurrent visual stimulation with 10 min/hr of maternal auditory stimulation successfully learned and remembered the call for 24 hr following hatching, but appeared to have forgotten the call by 48 hr of age. However, in the current experiment, chicks who received the same sensory stimulation regime during prenatal development

successfully learned and remembered the call until 48 hr following hatching, and entire day longer than chicks in Lickliter and Hellewell (1992) remembered the maternal call to which they had been exposed.

Interestingly, upon further examination of Lickliter and Hellewell's (1992) method, embryos were presented with 10 min/hr of visual stimulation, followed by a 20 minute interval, followed by 10 min/hr of bobwhite maternal Call B. In other words, the nonconcurrent amounts of visual and auditory stimulation were "spread out" within each hour of the 24 hr pre-hatching period. However, in the current experiment embryos were presented with 10 min/hr of visual stimulation, immediately followed by 10 min/hr of maternal auditory stimulation (maternal Call A or Call B). While it is somewhat surprising that these two different methods of providing stimulation to embryos appear to have some influence on chicks' learning ability, effects of similar variations in stimulation presentation have, in fact, been previously reported in recent work with bobwhite quail embryos. Sleigh and Lickliter (1998) recently found that embryos provided with 10 min/hr of bobwhite chick contentment calls immediately followed by 10 min/hr of bobwhite chick distress calls demonstrated an accelerated pattern of visual responsiveness to maternal cues. However, chicks exposed to distress calls immediately followed by contentment calls showed deficits in the normal pattern of visual responsiveness. These findings suggest that variations in prenatal sensory stimulation presentation in as short an interval as 20 minutes can have influential effects on chicks' subsequent responsiveness.

In summary, the results from the current experiment suggest that chicks can learn and remember a bobwhite maternal call for 48 hr following hatching when exposed to this call during the prenatal period. From this experiment and Lickliter and Hellewell's earlier results, it appears that nonconcurrent visual stimulation during embryonic development does not interfere with prenatal auditory learning. In fact, this enhanced visual stimulation, when provided sequentially with maternal auditory stimulation, may actually serve to strengthen embryos' learning or remembering of this information.

Experiment 4B: Effects of Prenatal Visual Stimulation + Auditory Experience, and Postnatal Attenuated Visual Stimulation on Auditory Learning

Lickliter and Hellewell (1992) report that while chicks receiving prenatal visual and auditory stimulation can learn the auditory information, these chicks forget the maternal call they learned prenatally by 48 hrs following hatching. In the previous experiment, it was demonstrated that chicks can remember the bobwhite maternal call to which they were exposed until 48 hr, when prenatal visual stimulation is provided sequentially with the maternal auditory information. However, based on these two studies, it appears that the maximum amount of time that chicks can remember a call following hatching is 48 hr. What experiences present during postnatal development might cause chicks to forget the call they learned during prenatal development? In light of the previous experiments in this study and Turkewitz and Kenny's (1982) sensory system interference hypothesis, it seems likely that postnatal visual experience could introduce a source of intersensory interference which leads to the overtaxing of newly hatched chicks' ability to remember the information they learned during prenatal development.

Therefore, this experiment examined how prenatal and postnatal visual experience affect bobwhite chicks' ability to remember information learned during prenatal development. The current experiment explored how attenuated postnatal visual experience influences chicks' ability to remember auditory information they learned during prenatal development during later stages of postnatal development (e.g., Experiment 4A; Lickliter & Hellewell, 1992). If postnatal visual experience causes chicks to forget auditory information that they learned prenatally, then attenuating visual experience during the postnatal period should enable chicks to demonstrate auditory learning for longer periods than chicks in Experiment 4A (who might have been susceptible to interference from visual experience).

Method

Subjects were 94 bobwhite quail embryos and hatchlings, drawn from five separate hatches to control for possible between-batch variation in subjects' behavior. Subjects in this experiment received the same experimental manipulations as chicks in Experiment 4A, except that they were reared in light-attenuated conditions following hatching. In other words, on day 21 of incubation, embryos underwent the egg-opening procedure as described in General Methods. Subjects were then socially incubated and received 10 min/hr patterned visual stimulation, followed by 10 min/hr of a recorded bobwhite maternal call (either Call A or Call B), each hour for the 24 hrs prior to hatching.

Following hatching, chicks were reared in groups of 10-14 conspecifics and placed in a darkened portable brooder from hatching until testing at 24, 48, 72, or 96 hrs ($n = 20$ in each group). 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. Chicks were tested in a simultaneous choice test between bobwhite maternal Call A and Call B. Immediately prior to testing, chicks were removed from the brooder and allowed to adjust their eyes to the light of the testing room for a period of 1-2 minutes, as in previous studies (Columbus & Lickliter, 1998; Lickliter, Lewkowitz, & Columbus, 1996).

Results and Discussion

Results are shown in Tables 11 and 12. Chicks exposed to 10 min/hr of nonconcurrent prenatal visual stimulation and 10 min/hr of bobwhite maternal stimulation, then reared in postnatal light-attenuated conditions demonstrated a significant preference for the familiar bobwhite maternal call at 48 hr ($\chi^2(2) = 9.0, p < .05$) and 96 hr ($\chi^2(2) = 8.86, p < .05$) following hatching. These patterns of individual preference were supported by analysis of latency and duration scores, with chicks showing significantly shorter latencies and longer durations to the familiar call at 48 hr ($z = 2.0$ for latency, $p < .05$, $z = 2.4$ for duration, $p < .01$) and longer durations in response to the familiar call at 96 hr ($z = 2.42, p < .01$).

Chicks failed to prefer the familiar call at 24 hr ($\chi^2(2) = 1.68, p > .05$) and 72 hr ($\chi^2(2) = 2.5, p > .05$) following hatching, and analysis of latency and duration scores further supported these results, with chicks showing no differences in latency to either call at 24 hr ($z = 1.29, p > .05$) and 72 hr ($z = 0.6, p > .05$), and no differences in duration

at 72 hr ($z = 1.12$, $p > .05$). However, chicks did demonstrate longer durations in their response to the familiar call at 24 hr ($z = 1.65$, $p < .05$).

These observed results do not support the hypothesis that chicks who received prenatal visual and auditory stimulation would learn and remember the call into later stages of postnatal development when the opportunity for postnatal visual experience was removed from chicks' rearing environment. Interestingly, chicks in this experiment did demonstrate memory for familiar prenatal auditory information at 48 and 96 hr following hatching, but not at 24 or 72 hr following hatching.

There are two important notes to make about these findings. First, they support the idea presented in Experiments 3A, 3B, and 3C that mismatches in prenatal and postnatal environments lead to delays in auditory learning. This hypothesis is supported by chicks' failure to prefer the familiar call at 24 hr in the present experiment. Chicks exposed to nonconcurrent prenatal visual experience and maternal auditory information typically learn and remember this call at 24 hr following hatching, when reared in postnatal lighted conditions (Experiment 3A; Lickliter & Hellewell, 1992). However, chicks in the present experiment who were exposed to nonconcurrent prenatal visual experience and maternal auditory information and were then reared in postnatal darkened conditions failed to demonstrate a preference for this learned information at 24 hr of age. It seems unlikely that chicks did not learn the information, as they did show a preference for the familiar call at 48 hr and 96 hr following hatching. What seems more likely based on the current findings is that their performance was impaired in some manner by the mismatch in prenatal lighted / postnatal darkened conditions.

Second, chicks in this experiment did demonstrate the ability to remember the maternal call they heard during prenatal development until 96 hr of age, a full four days following their final exposure to this call. Based on Turkewitz and Kenny's (1982) sensory limitations hypothesis, it seems likely that taking away competing sources of postnatal visual sensory stimulation might help chicks remember auditory information into later ages of postnatal development than chicks who are reared in the typical rearing environment (i.e., one that includes patterned visual experience). This finding is important, as all previous studies of auditory learning in bobwhite quail embryos and chicks have shown that the latest time in postnatal development that chicks demonstrate a preference for the familiar call is 48 hr following hatching (Experiment 4A). These findings would indicate that, given the right postnatal conditions, chicks can remember auditory information that they heard as embryos into relatively late stages of early postnatal development. Of course, this does not explain why chicks failed to demonstrate a preference for the familiar call at 72 hr. Future studies should examine this suppression/reemergence of preference pattern.

Experiment 4C: Effects of Prenatal Light-Attenuation + Maternal Call and Postnatal Light-Attenuation on Postnatal Auditory Memory

Findings from the previous experiment indicate that chicks who receive prenatal visual experience but attenuated postnatal visual experience can learn and remember a bobwhite maternal call until 96 hr following hatching. Based on results found in Experiment 4B and earlier studies of auditory learning in bobwhite quail (i.e., Lickliter & Hellewell, 1992), it would appear that chicks who received less overall amounts of visual

stimulation during postnatal development can remember prenatal auditory information into late stages of postnatal development (96 hr). However, chicks in Experiment 4B failed to demonstrate a preference for the familiar call at 24 hr, presumably because of the mismatch in prenatal and postnatal visual experience. This raises the possibility that taking away even more visual experience would create an optimal environment for both auditory learning prior to hatching and memory for this auditory information in the days following hatching.

In this light, the current experiment was designed to examine how visual attenuation during both prenatal and postnatal development might facilitate auditory learning in bobwhite quail embryos and hatchlings. Specifically, it was hypothesized that prenatal exposure to a particular bobwhite maternal call during the 24 hr prior to hatching in darkened conditions would allow embryos to successfully learn this auditory information. In fact, previous studies with bobwhite quail have demonstrated that embryos who hear auditory information during darkened conditions in the 24 hr prior to hatching successfully learn and remember this call at 24 hr (when reared in postnatal lighted conditions, see Lickliter & Hellewell, 1992; Sleight, Columbus, & Lickliter, 1996). It was hypothesized that postnatal rearing in light-attenuated conditions would allow chicks to remember the maternal call at all ages tested during postnatal development.

Method

Subjects were 86 bobwhite quail embryos and hatchlings, drawn from seven separate hatches to control for possible between-batch variation in subjects' behavior. Subjects in this experiment received the same experimental manipulations as chicks in Experiment 4B, except that they were reared in light-attenuated conditions prior to hatching. In other words, on day 21 of incubation, embryos underwent the egg-opening procedure as described in General Methods. Subjects were then socially incubated in darkness and received 10 min/hr of a recorded bobwhite maternal call (either Call A or Call B), for the 24 hrs prior to hatching.

Following hatching, chicks were reared in groups of 10-14 conspecifics and placed in a darkened portable brooder from hatching until testing at 24, 48, 72, or 96 hrs ($n = 20$ in each group). 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. Chicks were tested in a simultaneous choice test between bobwhite maternal Call A and Call B. Immediately prior to testing, chicks were removed from the brooder and allowed to adjust their eyes to the light of the testing room for a period of 1-2 minutes, as in previous studies (Columbus & Lickliter, 1998; Lickliter, Lewkowicz, & Columbus, 1996).

Results and Discussion

Results from this experiment are shown in Tables 11 and 12. As can be seen in the tables, chicks incubated in darkness with 10 min/hr of bobwhite maternal auditory information, then reared in postnatal light-attenuated conditions failed to demonstrate a significant preference for the familiar bobwhite call at 24 hr following hatching ($\chi^2(2) = 4.9, p > .05$). Analysis of latency and duration scores at 24 hr supported this pattern of individual preference, with chicks showing no differences in latency ($z = 0.17, p > .05$) or

duration scores ($z = 1.25$, $p > .05$) at this age. Chicks did, however, demonstrate a preference for the familiar call at 48 hr following hatching ($\chi^2 (2) = 7.63$, $p < .05$), but analysis of latency and duration scores did not support this pattern of preference ($z = 1.55$ for latency, $z = 0.67$ for duration, $p > .05$ in both cases), indicating that this pattern of preference for the familiar call was rather weak.

Interestingly, chicks demonstrated a significant preference for the unfamiliar call over the familiar call at 72 hr ($\chi^2 (2) = 6.1$, $p < .05$), but as in the 48 hr group, analysis of latency and duration scores did not support this preference, with chicks showing no differences in latency ($z = 0.93$, $p > .05$) or duration ($z = 0.9$, $p > .05$) in their response either call. These results suggest, as in the previous group, that chicks' observed preference for the unfamiliar call was weak. Finally, chicks tested at 96 hr also failed to demonstrate a significant preference for the familiar or unfamiliar call ($\chi^2 (2) = 1.37$, $p > .05$), and latency ($z = 0.87$, $p > .05$) and duration scores ($z = 0.68$, $p > .05$) further supported this lack of preference.

Results from the present experiment indicate that chicks who are reared in complete darkness during prenatal and postnatal development actually show deficits in their ability to learn maternal auditory information. This finding is contrary to my original predictions for chicks' learning and memory abilities. Specifically, I had previously expected that chicks who had competing visual sensory stimulation removed from their developmental niche would demonstrate facilitated auditory learning and memory. However, this was not the case.

These current results seem rather counterintuitive when viewed in light of Turkewitz and Kenny's (1982) sensory systems limitations hypothesis and Gottlieb, Tomlinson, and Radell's (1992) developmental intersensory interference hypothesis. Both of these views would argue against early visual experience having a facilitation effect on auditory functioning. However, in the present experiment embryos and hatchlings who were denied visual stimulation showed deficits in auditory learning and memory, whereas chicks who received moderate amounts of visual stimulation during prenatal development demonstrate facilitated auditory learning abilities (Experiments 4A, 4B; Lickliter & Hellewell, 1992).

When viewed collectively, the current findings from Experiments 4A, 4B, and 4C would suggest that the presence of visual stimulation and thus the opportunity for visual experience during prenatal development is vital for successful learning and memory of auditory information. In fact, the removal of visual stimulation for extended periods seems to inhibit or interfere with auditory learning abilities in bobwhite quail. These findings thus raise interesting questions for the actual role that visual experience plays in helping chicks consolidate information they learn during the perinatal period.

General Discussion

The current study examined how visual experience during prenatal and postnatal development affects bobwhite embryos' and hatchlings' ability to learn and remember maternal auditory vocalizations. More specifically, this project was designed to 1) examine how early learning capacity is affected by visual stimulation during perinatal development and 2) further test Turkewitz and Kenny's (1982) theory of competition within and between developing sensory systems. This theory was tested by altering the presence or absence of visual sensory stimulation within developing chicks' and embryos' developmental niches at varying points in either the prenatal period, the postnatal period, or both prenatal and postnatal periods, and then assessing embryos' or chicks' auditory learning abilities.

To review, Turkewitz and Kenny (1982) proposed that constraints inherent in the sequential onset of sensory functioning provide a powerful organization function for early perceptual development. From this view, limitations within the sensory modalities at differing points in developmental time provide a valuable structure within which each developing sensory system can fully develop with little interference from competing sensory systems. In addition to structuring development within a sensory system, these limitations are also thought to influence the development of relationships between sensory systems. Furthermore, these relationships are dynamic and changing at different times in development, and are influenced by the type, timing, and amount of sensory stimulation encountered (Gottlieb, Tomlinson, & Radell, 1989; Lickliter, 1993; Lickliter & Lewkowicz, 1995; Sleight & Lickliter, 1996).

Based on this theory and previous evidence supporting it, it was hypothesized that chicks would be able to learn a different maternal call than had been used in previous studies of auditory learning in bobwhite quail (Columbus & Lickliter, 1997; Lickliter & Hellewell, 1992). In light of Turkewitz and Kenny's theory, it was also hypothesized that premature visual experience would interfere with postnatal auditory learning, that attenuation of postnatal visual experience would facilitate postnatal auditory learning, and that both premature and postnatal visual experience would lead to severe deficits in auditory learning capacity. In the current examination of the effects of visual stimulation on memory, it was hypothesized that nonconcurrent premature visual experience would not interfere with prenatal auditory learning, but that postnatal visual experience would interfere with chicks' memory for auditory information encountered prenatally. Given this potential finding, I also hypothesized that attenuating postnatal visual experience would lead to an increased ability to remember prenatal auditory stimulation. As illustrated in Figures 1 and 2, the overall results of this study did not always match these hypothesized outcomes, and in some cases were opposite to what I had previously predicted.

I. POSTNATAL AUDITORY LEARNING

Experiments 1A and 1B revealed that chicks who were reared in both lighted and light-attenuated conditions demonstrate the ability to learn an individual maternal call, Call A, by the same ages as chicks in previous studies (Columbus & Lickliter, 1997), supporting my original hypothesis. These results indicate that exposure to either bobwhite maternal Call A or Call B (recorded from different bobwhite hens) leads to

parallel patterns of successful auditory learning. This finding is important, as it highlights that chicks are relatively malleable in their ability to learn specific maternal auditory information, an ability that would provide a useful and adaptive function within chicks' ecological niche during early development. These findings parallel previous studies within the human infant literature which have shown neonates to be particularly responsive to their own mother's voice during late prenatal and early postnatal development (Cooper & Aslin, 1990; DeCasper & Fifer, 1980) and to specific types of auditory information to which they have been exposed during prenatal development (DeCasper & Spence, 1986). These varied studies serve to demonstrate that young infants typically have a rather flexible and presumably adaptive ability to learn the specific forms of maternal auditory stimulation present within their own, individual developmental context.

II. PRENATAL EXPERIENCE AND POSTNATAL AUDITORY LEARNING

Results from Experiments 3A, 3B, and 3C in part seem to support Turkewitz and Kenny's (1982) sensory system limitations hypothesis that premature stimulation from a later-developing sensory system can lead to deficits in species-typical behavioral organization and development. This theory is particularly supported by results found with chicks in Experiment 3C, who received prenatal visual experience prior to hatching, then showed auditory learning delays during early postnatal development. It appears from results from this experiment that 24 hr of premature (i.e., prenatal) visual experience is sufficient to delay postnatal auditory learning by at least 24 hr.

Findings from Experiment 3C appear to support Turkewitz and Kenny's theory, but findings from Experiment 3A and 3B did not provide as strong evidence for the sensory systems limitations hypothesis. In particular, Experiment 3A results indicate that nonconcurrent premature visual experience may actually facilitate, rather than impair, postnatal auditory learning (when chicks are reared in lighted conditions), with chicks learning maternal auditory information as early as 24 hr following hatching. In addition, denying chicks' the opportunity for prenatal and postnatal visual stimulation (Experiment 3B) led to successful postnatal auditory learning. These results would appear to support Turkewitz and Kenny's hypothesis, but when viewed in conjunction with results from Experiment 3A, some explanation other than that proposed by Turkewitz and Kenny would seem more adequate for why chicks can learn auditory information equally well under these two very different sensory stimulation regimes.

Importantly, rather than impairing postnatal auditory learning, prenatal visual stimulation (as in Experiment 3A) appears to facilitate chicks' postnatal learning ability when matching visual stimulation is present during the postnatal period. Previous studies with bobwhite embryos have shown similar results, in that prenatal visual stimulation (as long as it falls within some optimal range, e.g., Sleigh & Lickliter, 1995), accelerates chicks' intersensory responsiveness. Similarly, Gottlieb, Tomlinson, and Radell (1989) found that nonconcurrent prenatal visual stimulation and exposure to duckling maternal auditory stimulation did not interfere with ducklings' ability to learn maternal auditory information. Furthermore, ducklings who were exposed to premature visual stimulation did not show deficits in their postnatal ability to learn a duckling maternal call. Research with bobwhite quail embryos and hatchlings has also reported similar findings. Lickliter

(1990a, 1990b) and Lickliter and Lewkowicz (1995) found that bobwhite embryos who were exposed to 10 min/hr of premature visual stimulation demonstrated accelerated patterns of postnatal auditory-visual responsiveness. Collectively, these studies have demonstrated that embryos who receive premature visual stimulation can show accelerated patterns of intersensory responsiveness. If premature visual experience facilitates postnatal perceptual responsiveness, it seems likely that this visual stimulation might also facilitate postnatal auditory learning as well, and the current results certainly seem to support this interpretation.

However, another possible explanation for the observed findings is that mismatches in the types of prenatal and postnatal sensory stimulation encountered interfered with chicks' perceptual development, a finding that has also been reported in previous studies with bobwhite quail embryos and hatchlings. McBride and Lickliter (1995) examined the role of the relationship between prenatal and postnatal stimulus cues in determining chicks' subsequent perceptual responsiveness. In that study, bobwhite embryos who were exposed to 10 min/hr of maternal auditory stimulation (Call B) and 10 min/hr of nonconcurrent prenatal visual stimulation preferred the familiar prenatal stimulus (Call B) over a novel auditory-visual stimulus (Call A + Bobwhite Maternal Hen) when tested at 24 hr following hatching. Similarly, embryos who were exposed to 10 min/hr of Call B and 10 min/hr of nonconcurrent prenatal visual stimulation (auditory-visual stimulation) subsequently preferred auditory-visual stimulation (matching stimulation) over auditory stimulation alone (a non-matching form of stimulation) when tested at 24 hr following hatching. McBride and Lickliter (1995) concluded that chicks appear to respond preferentially to postnatal auditory stimulation that most closely resembles their prenatal auditory experiences.

This "mismatch" hypothesis would potentially explain why Columbus and Lickliter (1997) found that chicks' postnatal auditory learning abilities are different when reared in lighted or light-attenuated conditions. In that study, chicks who received no prenatal manipulations (i.e., were incubated in the dark), who were then postnatally exposed to 10 min/hr of bobwhite maternal Call B in lighted conditions from hatching to testing failed to prefer that familiar Call B until 72 hr following hatching. On the other hand, chicks who received no prenatal manipulation (i.e., prenatal dark conditions), who were then exposed to 10 min/hr of bobwhite maternal Call B in darkened conditions demonstrated the ability to learn that call by 24 hr following hatching. In the case of prenatal dark then postnatal lighted conditions (a mismatch in prenatal and postnatal visual conditions), chicks demonstrated slower patterns of postnatal auditory learning than chicks reared in prenatal and postnatal darkened conditions (a match in prenatal and postnatal visual conditions).

The mismatch hypothesis would also explain the varied results of Experiment 3. Specifically, chicks in Experiment 3A, who were reared with prenatal and postnatal lighted conditions, and chicks in Experiment 3B, who were reared in prenatal and postnatal darkened conditions, all demonstrated the ability to learn by 24 hr following hatching, as did chicks in Columbus and Lickliter (1997). This finding is also supported by results from Experiment 3C, where chicks who were reared in prenatal lighted conditions but postnatal darkened conditions demonstrated delays in auditory learning, just as chicks who were reared in similar conditions in Columbus and Lickliter (1997). Findings from Experiments 3A, 3B, and 3C indicate that specific prenatal sensory

experiences affect chicks' ability to learn auditory information during postnatal development, and that mismatches in the type of stimulation encountered during prenatal and postnatal development may impair or interfere with postnatal auditory learning abilities.

Interestingly, the current results appear to support Gottlieb, Tomlinson, and Radell's (1989) "weak form" of developmental intersensory interference, rather than Turkewitz and Kenny's (1982) "strong form" of developmental intersensory interference. Gottlieb et al. (1989) distinguished between two types of intersensory interference. The strong form of interference, originally proposed by Turkewitz and Kenny suggests that any premature stimulation from a later-developing sensory modality can cause long-lasting or permanent reorganization of an organism's sensory system structure or organization. The weaker form of intersensory interference proposed by Gottlieb, Tomlinson, and Radell (1989) and Radell and Gottlieb (1992) suggests that premature stimulation from a later-developing sensory modality can cause transient interference effects by "overtaxing" the organism's developing but immature attentional abilities and sensory system organization.

In the current project, chicks who received premature visual stimulation and were subsequently reared in postnatal darkened conditions demonstrated a 24 hr delay in their responsiveness to the familiar call. This result suggests that premature visual stimulation interfered with postnatal auditory learning, but only temporarily, as chicks did eventually prefer the familiar maternal call by 48 hr following hatching (Experiment 3C). Taken together, the results from Experiments 3A, 3B, and 3C appear to more strongly support the "weak form" of developmental intersensory interference proposed by Gottlieb and his colleagues (Gottlieb, Tomlinson, & Radell, 1989; Radell & Gottlieb, 1992).

These findings also suggest that mismatches in type and amount of prenatal and postnatal stimulation may delay auditory learning during postnatal development. It is possible that greater differences between the type of prenatal and type of postnatal sensory stimulation encountered can create greater competition between chicks' developing sensory systems than when the overall amount or type of sensory stimulation is "spread out" between prenatal and postnatal development. Future studies should explore this intriguing possibility.

III. PRENATAL AUDITORY LEARNING AND POSTNATAL MEMORY

Results from Experiments 1A, 1B, 3A, 3B, and 3C of this project suggest several conclusions about the nature of precocial avian chicks' postnatal auditory learning. First, it appears that mismatches between prenatal and postnatal sensory experience interfere with chicks' ability to learn maternal auditory stimulation in the period following hatching, while matching amounts or levels of stimulation throughout perinatal development appear to maintain or facilitate auditory learning capacity. Second, rather than drastically or permanently altering chicks' learning ability, the effects of providing mismatching stimulation levels throughout prenatal and postnatal development appear to have transient effects on postnatal learning ability.

In this light, it would seem likely that providing embryos with matching prenatal and postnatal experiential histories would lead to similar effects. However, results from Experiments 4A, 4B, and 4C clearly do not support the conclusions made from the

postnatal auditory learning experiments outlined above. Chicks who were incubated with 10 min/hr of maternal auditory stimulation (Call A or Call B) and 10 min/hr of nonconcurrent prenatal visual stimulation (and then reared in lighted conditions postnatally) demonstrated the ability to learn and remember the call to which they had been exposed prenatally until at least 48 hr following hatching (Experiment 4A). This particular finding also supports the “weak form” of developmental intersensory interference. Specifically, premature visual stimulation did not appear to interfere with prenatal auditory learning, as long as the visual stimulation was presented nonconcurrently. These results also parallel findings from previous studies of prenatal auditory learning in ducklings (Gottlieb, et al., 1989; Radell & Gottlieb, 1992) and quail (Lickliter & Hellewell, 1992; McBride & Lickliter, 1995).

Interestingly, the findings from Experiment 4A also support the matching hypothesis proposed by McBride and Lickliter (1995). In the current case, embryos who had the opportunity for both prenatal and postnatal visual experience demonstrated successful prenatal auditory learning and postnatal memory for this auditory information until 2 days following hatching, but appeared to forget the familiar maternal call by 72 hr following hatching. Why did chicks’ fail to remember the prenatally heard information? It is possible that visual stimulation encountered during the postnatal rearing environment led to interference with chicks’ memory for the maternal auditory stimulation they encountered as embryos. A more likely explanation, however, is that 24 hr of prenatal exposure is simply not enough information to maintain chicks’ preference for this call into later ages of postnatal development. It is important to highlight that in Experiments 3A – 3C, chicks received as much as 3 times the overall amount of total exposure time to the individual maternal call as did embryos in the prenatal auditory learning experiments. In other words, it is possible that if chicks had continuous experience with the particular form of maternal auditory information they heard as embryos into the postnatal period, they might be able to successfully remember the call into later stages of development. Future studies should examine the effects of continued experience across prenatal and postnatal periods on postnatal memory capacity. What also remains to be explored are the specific amounts of prenatal and postnatal exposure that are needed to maintain chicks’ preference for prenatally experienced auditory information.

What was also interesting in the investigation of prenatal auditory learning in Experiment 4 was the finding that reducing the amount of visual stimulation available during postnatal development served to extend the amount of time that chicks could remember the maternal call heard during incubation (Experiment 4B). Chicks who were reared with 10 min/hr nonconcurrent prenatal visual stimulation and 10 min/hr of maternal Call A or Call B and were subsequently reared in postnatal darkened conditions could remember the familiar call at least through 96 hr following hatching. This finding demonstrates that, given the right conditions, chicks can successfully remember information they heard as embryos into relatively late stages of early postnatal development (i.e., 96 hr). Other studies of prenatal auditory learning in bobwhite quail have found that the longest time period chicks can remember prenatally experienced information is approximately 48 hr following hatching (Experiment 4A). However, the findings of Experiment 4B suggest that reducing the overall amount of postnatal visual stimulation can extend chicks’ ability to remember prenatal auditory information, and lend support to Turkewitz and Kenny’s (1982) intersensory interference hypothesis.

However, what is perplexing about these findings is that chicks appeared to forget the call at 24 hr and 72 hr following hatching, while remembering it at 48 and 96 hr. Again, it seems unlikely that chicks failed to learn the call, as they did recognize and prefer the familiar call at 48 and 96 hr following hatching. What factors led to these observed patterns of preference for the familiar call? One possible explanation is that chicks failed to remember the call at 24 hr because they experienced mismatched prenatal and postnatal sensory experiences. Other experiments in this project demonstrated that chicks who are reared with prenatal visual stimulation and postnatal visual stimulation successfully learn the call at 24 hr regardless of whether they heard the call postnatally (Experiment 3A) or prenatally (Experiment 4A). However, chicks in Experiment 4B did not demonstrate a preference for the familiar maternal call at 24 hr, indicating that some interference with learning and/or memory occurred. It seems likely that chicks' performance was delayed in some way by the mismatch in prenatal and postnatal visual stimulation at 24 hrs, although this explanation fails to explain why chicks did not remember the familiar call at 72 hr following hatching. Therefore, the mechanisms underlying this observed pattern of suppression and reemergence of preference remain to be explored in future studies.

One possible explanation for the observed pattern of results in Experiment 4 is that chicks reared in postnatal darkness experienced increased stress levels as a result of this atypical rearing environment. Recently de Quervain, Roozendaal, and McGaugh (1998) showed that stress associated with subsequent increases in glucocorticoid levels in rats affects memory retrieval. In this study, rats were trained to navigate a water-maze spatial task. Rats who were given a footshock 30 minutes prior to testing demonstrated increased glucocorticoid levels and impaired task performance. However, rats who were shocked 2 minutes or 4 hours prior to testing (who had normal levels of glucocorticoids) demonstrated successful navigational abilities. Importantly, non-stressed rats who were injected with corticosterone 30 minutes prior to testing showed poor maze-navigation performance, similar to rats who were shocked 30 minutes prior to testing. Additionally, rats who were shocked 30 minutes prior to testing, but who had blocked corticosterone synthesis demonstrated successful task performance. These results suggest that stress, and subsequent increased glucocorticoid levels associated with stress, may impair retention of memories in a testing situation. Importantly, rats demonstrated temporary deficits in their ability to remember the maze-running task concurrent with increased cortisol levels (de Quervain, Roozendaal, & McGaugh, 1998). It is possible that in the present study, the observed patterns of suppression and reemergence in chicks' ability to remember information heard during prenatal development might have been reflective of their stressful postnatal rearing environment. Future studies could examine more closely the effects that organismic factors (such as increased hormone levels) have in forgetting in precocial birds.

The results from Experiment 4B also support Gottlieb's "weak form" of intersensory interference. Specifically, removing a competing source of stimulation (i.e., postnatal visual stimulation) allowed chicks to remember information for longer periods (Experiment 4B) than when chicks were reared in lighted conditions (Experiment 4A). Gottlieb's hypothesis does not, however, explain findings from Experiment 4C, in which embryos and chicks who were reared with an absence of patterned visual stimulation throughout perinatal development failed to successfully learn and/or remember auditory

information encountered during prenatal incubation. Based on the developmental intersensory interference hypothesis, chicks should have been able to remember prenatal auditory information following hatching. However, chicks reared in prenatal darkened conditions with 10 min/hr of maternal auditory stimulation failed to successfully learn and/or remember the familiar call at all ages tested. In fact, chicks at 72 hr demonstrated a significant preference for the non-familiar call. The mismatch hypothesis outlined above (see also McBride & Lickliter, 1995) also fails to explain this pattern of learning and memory. According to this hypothesis, chicks who were reared in prenatal and postnatal darkened conditions should have been able to successfully learn and/or remember the familiar call during postnatal development.

The fact that neither the developmental intersensory interference nor the mismatch hypotheses explain the obtained results leads me to conclude that some other mechanism influenced chicks' observed patterns of learning and memory. It is possible that the decreased levels of overall amount of stimulation in chicks' rearing environment in Experiment 4A led to chicks' poor ability to learn and remember auditory information. Previous studies with bobwhite embryos and hatchlings have indicated that chicks who are reared with substantially attenuated sensory stimulation (Columbus & Lickliter, 1998; Lickliter & Lewkowicz, 1995) demonstrate subsequent deficits in intersensory responsiveness and prenatal auditory learning ability. In light of these previous studies, it seems likely that the greatly attenuated overall levels of stimulation in Experiment 4C fell outside the optimal range of stimulation necessary for the maintenance of normal patterns of perceptual responsiveness and early auditory learning and memory. Specifically, chicks were reared with dramatically attenuated visual stimulation during prenatal and postnatal development might have displayed deficits in learning because they did not experience adequate amounts of overall sensory stimulation during perinatal development.

In conclusion, it appears that mismatches in the types of prenatal and postnatal sensory stimulation can lead to interference with auditory learning, while matches (that occur within some optimal range of overall amount of stimulation) can lead to successful or facilitated patterns of auditory learning. Finally, when viewed in conjunction with results from Experiments 3A, 3B, and 3C, it appears that the weak form of Gottlieb, Tomlinson, and Radell's (1992) intersensory interference hypothesis is more applicable to explaining the current findings than is the strong form originally proposed by Turkewitz and Kenny (1982).

IV. FUTURE DIRECTIONS

The current study examined the effects that changes in overall amount and timing of visual experience have on auditory learning. What remains to be explored is the effect(s) that augmented postnatal auditory stimulation may have on hatchlings' postnatal visual responsiveness. Several previous studies with bobwhite quail have indicated that particular types of substantially augmented auditory stimulation results in delays in postnatal auditory-visual responsiveness. Sleight and Lickliter (1996) exposed embryos to slightly augmented amounts of bobwhite chick contentment calls during incubation. Chicks receiving this auditory stimulation subsequently had accelerated patterns of auditory-visual responsiveness, but delayed patterns of auditory responsiveness.

Recently, Sleigh, Columbus, and Lickliter (1998) demonstrated that chicks who are exposed to augmented postnatal maternal auditory stimulation show delayed patterns of intersensory responsiveness. Future studies should more fully explore the role that augmented amounts of postnatal auditory stimulation plays in chicks' perceptual preferences and abilities.

This project also focused on how particular sensory experiences present within a specific environment affected chicks' auditory learning ability. However, in light of the findings from Experiments 4A, 4B, and 4C, it is possible that organismic factors such as chicks' overall levels of arousal, stress levels, or motor constraints contributed to the observed patterns of responsiveness to the familiar maternal call. What remains to be explored is how the various sensory stimulation regimes employed in this study affect chicks' physiological organization and responsiveness and their effects on subsequent learning ability. Such an approach would examine how learning affects both physiology and behavior, a strategy that is fully consistent with an ecological approach to learning and development.

V. PRENATAL AND POSTNATAL LEARNING AND MEMORY: THE BIG PICTURE

In a broader scheme, bobwhite embryos and chicks in this project demonstrated a remarkably robust ability to learn maternal auditory information under a wide variety of experiential conditions. This conclusion is supported by the fact that quail chicks demonstrated the ability to learn and remember an individual maternal call under all of the following conditions: (a) in their species-typical postnatal rearing environment, (b) in the presence and absence of premature prenatal visual stimulation, (c) in light-attenuated postnatal rearing conditions, and (d) in prenatal and postnatal light-attenuated conditions. These findings indicate that chicks' ability to learn is malleable in nature, and that chicks can learn maternal auditory information under a wide range of experiential situations and conditions. This propensity to learn within a large range of rearing conditions would certainly suggest that chicks' early auditory responsiveness is surprisingly well developed. It is, however, also surprisingly sensitive to the influence of the visual system, as demonstrated by the various experiments of this study.

Furthermore, the results of this project support the idea that there are multiple pathways to the same outcome in behavioral development. This notion of equifinality, which was originally proposed by Driesch (1929), supports a nonlinear, nondeterministic view of development, and has recently been supported by several recent studies utilizing avian species (Banker & Lickliter, 1993; Lickliter & Lewkowicz, 1995; Miller, Hicinbotham, & Blaich, 1990). For example, Banker and Lickliter (1993) examined the relative impact of early versus delayed visual experience on bobwhite embryo and quail intersensory development. Embryos who were exposed to 10 min/hr of premature visual experience during the 24 hr period prior to hatching, but were denied postnatal visual experience (by means of eye patches) from hatching until testing. Findings revealed that hatchlings responded to bobwhite maternal auditory-visual cues at similar ages as non-manipulated bobwhite chick controls. In other words, quail who received unusually early visual stimulation followed by species-atypical, darkened postnatal rearing conditions

demonstrated the same pattern of perceptual responsiveness as bobwhite embryos and hatchlings who received no experiential manipulations.

Findings from Lickliter and Hellewell (1992) also support this notion of equifinality. In that study, bobwhite embryos who were exposed to 10 min/hr nonconcurrent prenatal bobwhite maternal auditory stimulation and 10 min/hr patterned visual stimulation successfully learned the bobwhite maternal call. Embryos who did not receive any prenatal visual stimulation also successfully learned their familiar call. Importantly, these two differing sensory stimulation experiences led to the same outcome of successful auditory learning. Finally, Miller and colleagues (Miller, et al., 1990) demonstrated that duckling embryos who received prenatal auditory experience or altered postnatal social experience showed similar patterns of freezing responses to the duckling maternal alarm call.

Results from these experiments support the growing body of evidence that the sensory systems are strongly linked throughout the perinatal period, and that stimulation to one sensory modality can affect infants' processing of information from other sensory modalities. Additionally, results found in this study provide at least partial answers to the questions raised at the beginning of this project, namely: 1) is prenatal learning different from postnatal learning? 2) what is the nature of the relationship between prenatal and postnatal learning, and the role of experience in shaping this relationship? and 3) does visual system experience during postnatal development influence forgetting of auditory information learned prenatally, and interfere with processing of auditory information provided postnatally? As we have seen, prenatal learning patterns do appear different from postnatal learning patterns. Second, the particular types, amounts, and combination of experience encountered during perinatal development certainly seems to play a large role in shaping exactly how information is both learned and remembered during early development. Finally, premature visual experience can interfere slightly with postnatal auditory learning (when this learning occurs within different postnatal conditions) but in other conditions may serve to facilitate postnatal learning. However, the absence of visual experience during both prenatal and postnatal development seems to impair consolidation and memory of information encountered during prenatal development.

In the most general sense, results from this study support the notion that developmental outcomes emerge out of the interactions between a structured organism and a structured environment. As stated earlier, it has been suggested by several theorists that any understanding of learning and developmental processes must necessarily include the assumption that organisms and their respective environments interact throughout time, leading to predictable, stable, and hierarchically organized patterns of behavior (Germana, 1989; Gottlieb, 1983; Johnston, 1985; Johnston & Pietrewicz, 1985; Kuo, 1967; Lickliter, 1996, in press). In particular, Kuo (1967) has argued that any analysis of behavior is only complete if it relies on three primary variables: the physiology of the organism, the organism's current environmental setting, and the organism's individual developmental history. Early learning capacity in precocial infants seems dependent on both their developmental context and their previous individual experiences, notions that are central to an ecological approach to understanding behavioral development.

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Table 1. Summary of Results from Experiments 1A – 3C.

	Age	n	Preference
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Experiment 1A: POSTNATAL LIGHT + CALL A			
	72	20	CALL A
	96	20	CALL A
Experiment 1B: POSTNATAL DARK + CALL A			
	24	21	CALL A
	48	20	CALL A
	72	20	CALL A
	96	22	CALL A
Experiment 2: PRENATAL LIGHT CONTROL			
	24	20	NO PREFERENCE
	48	20	NO PREFERENCE
	72	20	NO PREFERENCE
	96	26	NO PREFERENCE
Experiment 3A: PRENATAL LIGHT / POSTNATAL LIGHT + MATERNAL CALL			
	24	20	FAMILIAR CALL
	48	20	FAMILIAR CALL
	72	20	FAMILIAR CALL
	96	22	FAMILIAR CALL
Experiment 3B: PRENATAL DARK / POSTNATAL DARK + MATERNAL CALL			
	24	20	FAMILIAR CALL
	48	20	FAMILIAR CALL
	72	20	FAMILIAR CALL
	96	26	FAMILIAR CALL
Experiment 3C: PRENATAL LIGHT / POSTNATAL DARK + MATERNAL CALL			
	24	20	NO PREFERENCE
	48	20	FAMILIAR CALL
	72	21	FAMILIAR CALL
	96	23	FAMILIAR CALL
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Table 2. Summary of Results from Experiments 4A – 4C.

	Age	n	Preference
Experiment 4A: PRENATAL LIGHT + MATERNAL CALL / POSTNATAL LIGHT			
	24	20	FAMILIAR CALL
	48	20	FAMILIAR CALL
	72	20	NO PREFERENCE
	96	20	NO PREFERENCE
Experiment 4B: PRENATAL LIGHT + MATERNAL CALL / POSTNATAL DARK			
	24	20	NO PREFERENCE
	48	20	FAMILIAR CALL
	72	29	NO PREFERENCE
	96	25	FAMILIAR CALL
Experiment 4C: PRENATAL DARK + MATERNAL CALL / POSTNATAL DARK			
	24	21	NO PREFERENCE
	48	20	FAMILIAR CALL
	72	24	NON-FAMILIAR CALL
	96	21	NO PREFERENCE

Table 3. Preference of Chicks in Simultaneous Auditory Choice Tests from Previous Studies (Columbus & Lickliter, 1997).

Age (in hrs)	n	n responding	Preference		
			Bobwhite Maternal Call A	Bobwhite Maternal Call B	No Preference
EXPERIMENT 1A: CONTROL					
24	20	19	4	6	9
48	20	18	2	8	8
72	20	16	4	8	4
96	20	16	4	4	8
EXPERIMENT 1B: POSTNATAL EXPERIENCE WITH "CALL B"					
24	20	20	4	8	8
48	20	18	1	11*	7
72	20	20	1	13**	6
96	20	18	0	18***	0
EXPERIMENT 2A: DARK-REARED CONTROL					
24	20	18	3	9	6
48	20	16	3	8	5
72	20	14	3	8	3
96	20	16	3	9	5
EXPERIMENT 2B: DARK-REARED/POSTNATAL EXPERIENCE WITH "CALL B"					
24	20	20	5	13**	2
48	20	19	1	15***	3
72	20	20	2	17***	1
96	20	17	1	16***	0

*** p < .001 (Chi-Square Test)

** p < .01 (Chi-Square Test)

* p < .05 (Chi-Square Test)

Table 4. Mean Latency and Duration Scores of Chicks in Simultaneous Auditory Choice Tests in Previous Studies (Columbus & Lickliter, 1997).

Age (in hrs)	n	Latency		Duration	
		Bobwhite Maternal Call A	Bobwhite Maternal Call B	Bobwhite Maternal Call A	Bobwhite Maternal Call B
EXPERIMENT 1A: CONTROL					
24	19	108.53	75.32	46.26	58.11
48	18	106.22	93.56	26.22	48.83*
72	16	131.00	78.38	49.94	49.06
96	20	49.69*	100.50	43.50	36.81
EXPERIMENT 1B: POSTNATAL EXPERIENCE WITH "CALL B"					
24	20	109.20	47.20	46.60	75.45
48	18	114.50	59.06	27.61	62.00*
72	20	188.95	50.65**	13.30	121.70***
96	20	210.65	24.45***	10.05	101.40***
EXPERIMENT 2A: DARK-REARED CONTROL					
24	18	137.39	44.17*	33.72	57.72
48	16	132.88	80.38	33.00	51.81
72	16	140.75	25.44**	30.00	49.81
96	16	75.94	71.88	41.63	37.44
EXPERIMENT 2B: DARK-REARED WITH "CALL B" EXPERIENCE					
24	20	194.70	101.95*	46.15	110.30*
48	19	241.32	63.21**	15.63	99.74**
72	20	169.80	51.40*	20.35	70.80*
96	17	238.41	69.71**	6.94	98.76***
*** p < .001 (Wilcoxon Signed-Ranks Test)					
** p < .01 (Wilcoxon Signed-Ranks Test)					
* p < .05 (Wilcoxon Signed-Ranks Test)					

Table 5. Preference of Chicks in Simultaneous Auditory Choice Tests in Experiments 1A & 1B.

Age (in hrs)	n	n responding	Preference		
			Bobwhite Maternal Call A (familiar)	Bobwhite Maternal Call B (unfamiliar)	No Preference
EXPERIMENT 1A: POSTNATAL CALL A EXPERIENCE (LIGHT)					
72	20	18	17***	0	1
96	20	19	18***	0	1
EXPERIMENT 1B: POSTNATAL CALL A EXPERIENCE (DARK)					
24	21	20	12*	4	4
48	20	20	19***	0	1
72	20	19	15***	1	3
96	22	19	18***	0	1

*** p < .001 (Chi-Square Test)

** p < .01 (Chi-Square Test)

* p < .05 (Chi-Square Test)

Table 6. Means and Standard Deviations of Latency and Duration Scores of Chicks in Simultaneous Auditory Choice Tests in Experiments 1A and 1B.

Age (in hrs)	n	Latency		Duration	
		Bobwhite Maternal Call A	Bobwhite Maternal Call B	Bobwhite Maternal Call A	Bobwhite Maternal Call B
EXPERIMENT 1A: POSTNATAL CALL A EXPERIENCE (LIGHT)					
72	18	48.44*** (54.41)	288.67 (48.08)	118.06*** (63.90)	1.33 (5.66)
96	19	45.37*** (40.79)	229.68 (121.42)	110.26*** (56.82)	5.26 (9.37)
EXPERIMENT 1B: POSTNATAL CALL A EXPERIENCE (DARK)					
24	20	51.80** (37.72)	168.75 (137.70)	94.85* (69.00)	31.65 (46.38)
48	20	44.55*** (38.95)	260.95 (95.68)	147.10*** (76.55)	8.95 (24.07)
72	19	47.84** (70.00)	174.79 (136.32)	104.53*** (67.11)	13.42 (24.01)
96	19	55.11*** (51.02)	229.95 (121.11)	103.63*** (60.90)	5.16 (9.06)

*** p < .001 (Wilcoxon Signed-Ranks Test)

** p < .01 (Wilcoxon Signed-Ranks Test)

* p < .05 (Wilcoxon Signed-Ranks Test)

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

Age (in hrs)	n	n responding	Preference		
			Bobwhite Maternal Call A	Bobwhite Maternal Call B	No Preference
EXPERIMENT 2: PRENATAL VISUAL EXPERIENCE					
24	20	18	4	4	10
48	20	17	5	6	6
72	20	18	6	6	6
96	26	18	5	8	5

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

Age (in hrs)	n	Latency		Duration	
		Bobwhite Maternal Call A	Bobwhite Maternal Call B	Bobwhite Maternal Call A	Bobwhite Maternal Call B
EXPERIMENT 2: PRENATAL VISUAL EXPERIENCE					
24	18	92.67 (103.35)	95.17 (100.82)	70.00 (60.84)	63.72 (54.72)
48	17	45.88 (69.51)	81.12 (88.59)	53.53 (64.08)	45.82 (37.19)
72	18	123.17 (104.51)	115.39 (110.83)	56.11 (52.13)	52.11 (51.86)
96	18	147.67 (128.25)	125.83 (105.61)	29.78 (48.30)	52.50 (59.39)

Table 9. Preference of Chicks in Simultaneous Auditory Choice Tests in Experiments 3A, 3B, and 3C.

Age (in hrs)	n	n responding	Preference		
			Familiar Bobwhite Maternal Call	Unfamiliar Bobwhite Maternal Call	No Preference
EXPERIMENT 3A: PRENATAL VISUAL / POSTNATAL CALL (LIGHT)					
24	20	19	14***	4	1
48	20	19	11*	2	6
72	20	20	20***	0	0
96	22	18	17***	0	1
EXPERIMENT 3B: PRENATAL DARK + POSTNATAL CALL (DARK)					
24	20	19	14***	3	2
48	20	15	11**	1	3
72	20	20	16***	1	3
96	26	24	16**	3	5
EXPERIMENT 3C: PRENATAL VISUAL / POSTNATAL CALL (DARK)					
24	20	19	11	5	3
48	20	20	14**	3	3
72	21	20	18***	0	2
96	23	20	17***	0	3

*** p < .001 (Chi-Square Test)

** p < .01 (Chi-Square Test)

* p < .05 (Chi-Square Test)

Table 10. Means and Standard Deviations of Latency and Duration Scores of Chicks in Simultaneous Auditory Choice Tests in Experiments 3A, 3B, and 3C.

Age (in hrs)	n	Latency		Duration	
		Familiar Bobwhite Maternal Call	Unfamiliar Bobwhite Maternal Call	Familiar Bobwhite Maternal Call	Unfamiliar Bobwhite Maternal Call
EXPERIMENT 3A: PRENATAL VISUAL + POSTNATAL CALL (LIGHT)					
24	19	89.00** (100.69)	210.58 (116.53)	138.16* (92.63)	43.17 (75.04)
48	19	60.84** (88.98)	183.21 (131.82)	94.89* (64.48)	44.47 (67.07)
72	20	45.55*** (34.14)	267.90 (81.91)	129.75*** (47.71)	2.85 (7.19)
96	18	32.06*** (29.53)	240.39 (115.06)	106.33*** (46.31)	4.83 (10.30)
EXPERIMENT 3B: PRENATAL DARK + POSTNATAL CALL (DARK)					
24	19	60.84** (79.83)	197.84 (128.40)	108.16** (81.34)	26.84 (46.89)
48	15	58.13** (60.79)	226.87 (125.70)	100.80** (78.53)	17.87 (36.95)
72	20	52.80*** (35.28)	237.60 (111.38)	138.15*** (76.32)	17.40 (45.30)
96	24	53.50*** (66.89)	187.00 (123.67)	82.33*** (73.95)	15.96 (28.22)
EXPERIMENT 3C: PRENATAL VISUAL + POSTNATAL CALL (DARK)					
24	19	128.95 (115.42)	142.58 (139.00)	113.53 (92.54)	66.68 (98.75)
48	20	62.10 (88.59)	147.65 (141.68)	110.50* (86.10)	43.15 (84.22)
72	20	28.20*** (23.01)	235.80 (115.30)	117.45*** (62.09)	8.35 (23.83)
96	20	54.50*** (70.63)	236.60 (111.13)	90.15*** (66.21)	11.20 (23.45)

*** p < .001 ** p < .01 * p < .05 (Wilcoxon Signed-Ranks Test)

Table 11. Preference of Chicks in Simultaneous Auditory Choice Tests in Experiments 4A, 4B, and 4C.

Age (in hrs)	n	n responding	Preference		
			Familiar Bobwhite Maternal Call	Unfamiliar Bobwhite Maternal Call	No Preference
EXPERIMENT 4A: PRENATAL CALL (LIGHT) + POSTNATAL LIGHT					
24	20	20	12*	6	2
48	20	20	13*	4	3
72	20	18	8	2	8
96	20	18	9	3	6
EXPERIMENT 4B: PRENATAL CALL (LIGHT) + POSTNATAL DARK					
24	20	19	9	5	5
48	20	18	12*	3	3
72	29	20	10	5	5
96	21	18	13*	6	2
EXPERIMENT 4C: PRENATAL CALL (DARK) + POSTNATAL DARK					
24	21	20	11	6	3
48	20	16	10*	5	1
72	21	20	7	11*	2
96	21	19	8	4	7

*** p < .001 (Chi-Square Test)

** p < .01 (Chi-Square Test)

* p < .05 (Chi-Square Test)

Table 12. Means and Standard Deviations of Latency and Duration Scores of Chicks in Simultaneous Auditory Choice Tests in Experiments 4A, 4B, and 4C.

Age (in hrs)	n	Latency		Duration	
		Familiar Bobwhite Maternal Call	Unfamiliar Bobwhite Maternal Call	Familiar Bobwhite Maternal Call	Unfamiliar Bobwhite Maternal Call
EXPERIMENT 4A: PRENATAL CALL (LIGHT) + POSTNATAL LIGHT					
24	20	110.90 (112.22)	182.45 (120.88)	120.30* (99.49)	50.25 (77.67)
48	20	104.90* (110.28)	176.65 (123.42)	106.80* (81.72)	48.80 (69.83)
72	18	65.17 (91.65)	108.28 (111.73)	71.28* (54.13)	39.11 (39.40)
96	18	95.67 (102.36)	137.50 (122.24)	72.06* (69.99)	24.89 (23.31)
EXPERIMENT 4B: PRENATAL CALL (DARK) + POSTNATAL DARK					
24	19	94.63 (96.06)	131.84 (133.10)	86.47 (72.17)	37.68 (47.39)
48	18	76.67* (105.97)	190.39 (138.26)	90.67** (95.59)	22.89 (52.01)
72	20	89.75 (115.87)	117.15 (119.29)	54.80 (52.34)	43.75 (71.27)
96	21	81.29 (113.79)	144.43 (132.05)	53.86** (51.47)	17.14 (19.07)
EXPERIMENT 4C: PRENATAL CALL (DARK) + POSTNATAL DARK					
24	20	94.60 (110.31)	111.10 (122.80)	78.80 (76.71)	50.25 (70.29)
48	16	109.25 (126.71)	185.06 (130.45)	99.50 (100.03)	69.75 (91.85)
72	20	178.55 (116.76)	110.10 (116.79)	42.10 (62.23)	63.85 (70.95)
96	19	84.32 (102.27)	126.26 (131.11)	42.11 (47.18)	30.16 (42.96)

*** p < .001 ** p < .01 * p < .05 (Wilcoxon Signed-Ranks Test)

	Hours Posthatching			
	24	48	72	96
Experiment 1A (Postnatal Call A/Light)			■	■
Experiment 1B (Postnatal Call A/Dark)	■	■	■	■
Experiment 2 (Prenatal Visual Control)	□	□	□	□
Experiment 3A (Prenatal Visual/ Postnatal Call+ Light)	□	□	□	■
Experiment 3B (Prenatal Dark/ Postnatal Call+Dark)	■	■	■	■
Experiment 3C (Prenatal Visual/ Postnatal Call+Dark)	□	□	■	■
Experiment 4A (Prenatal Visual+Call/ Postnatal Light)	■	□	□	□
Experiment 4B (Prenatal Visual+Call/ Postnatal Dark)	■	■	■	■
Experiment 4C (Prenatal Dark+Call/ Postnatal Dark)	■	■	■	■

= Hypothesized Absence of Auditory Preference
 = Hypothesized Demonstration of Auditory Learning

Figure 1. Summary of Hypothesized Presence or Absence of Auditory Learning Capacity in Experiments 1A – 4C.

	Hours Posthatching			
	24	48	72	96
Experiment 1A (Postnatal Call A/Light)			■	■
Experiment 1B (Postnatal Call A/Dark)	■	■	■	■
Experiment 2 (Prenatal Visual Control)	□	□	□	□
Experiment 3A (Prenatal Visual/ Postnatal Call+ Light)	■	■	■	■
Experiment 3B (Prenatal Dark/ Postnatal Call+Dark)	■	■	■	■
Experiment 3C (Prenatal Visual/ Postnatal Call+Dark)	□	■	■	■
Experiment 4A (Prenatal Visual+Call/ Postnatal Light)	■	■	□	□
Experiment 4B (Prenatal Visual+Call/ Postnatal Dark)	□	■	□	■
Experiment 4C (Prenatal Dark+Call/ Postnatal Dark)	□	■	▨	□

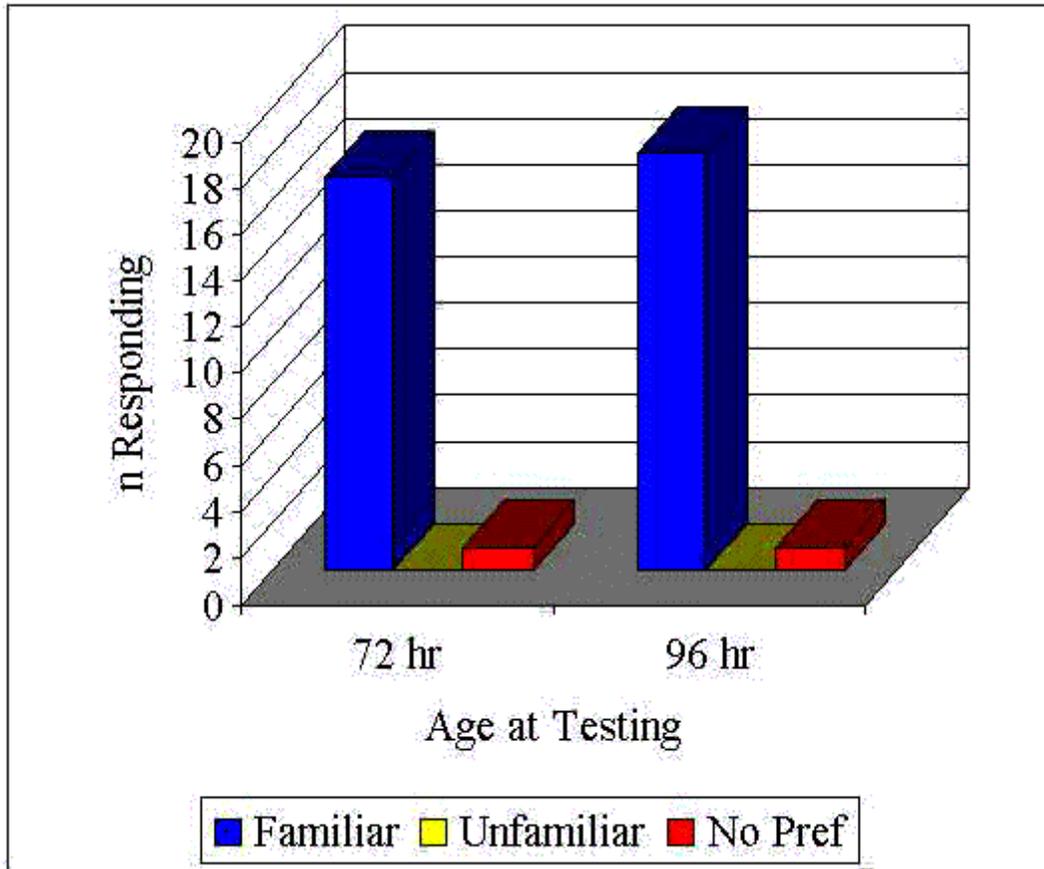
□ = Absence of Auditory Preference

■ = Preference for Familiar Call

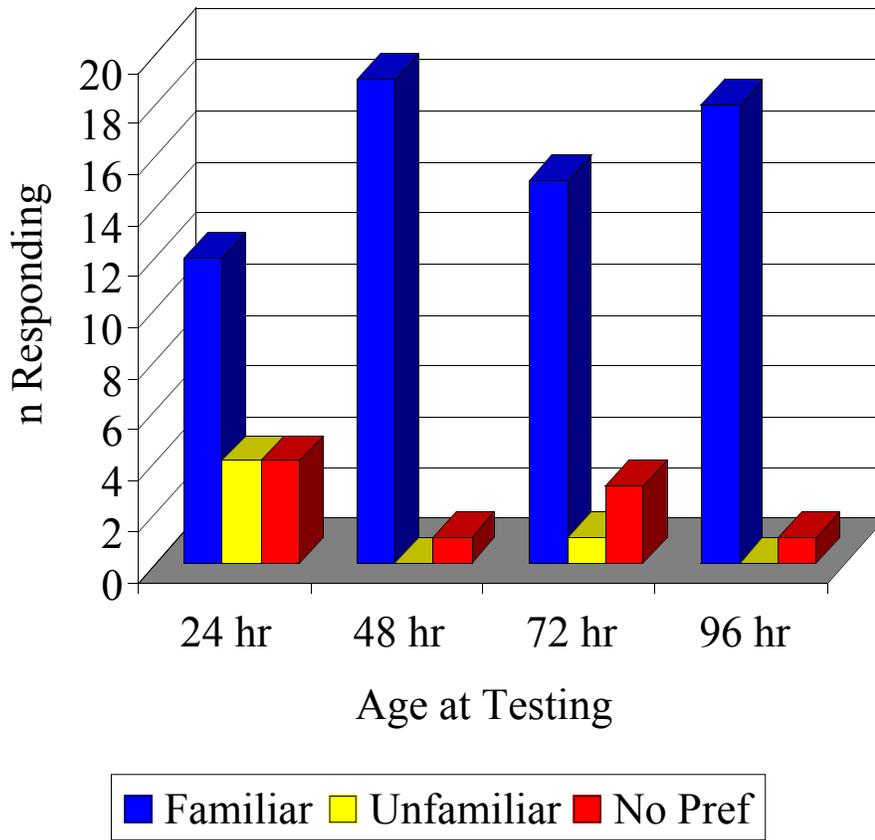
▨ = Preference for Unfamiliar Call

Figure 2. Summary of Actual Results of Experiments 4A – 4C.

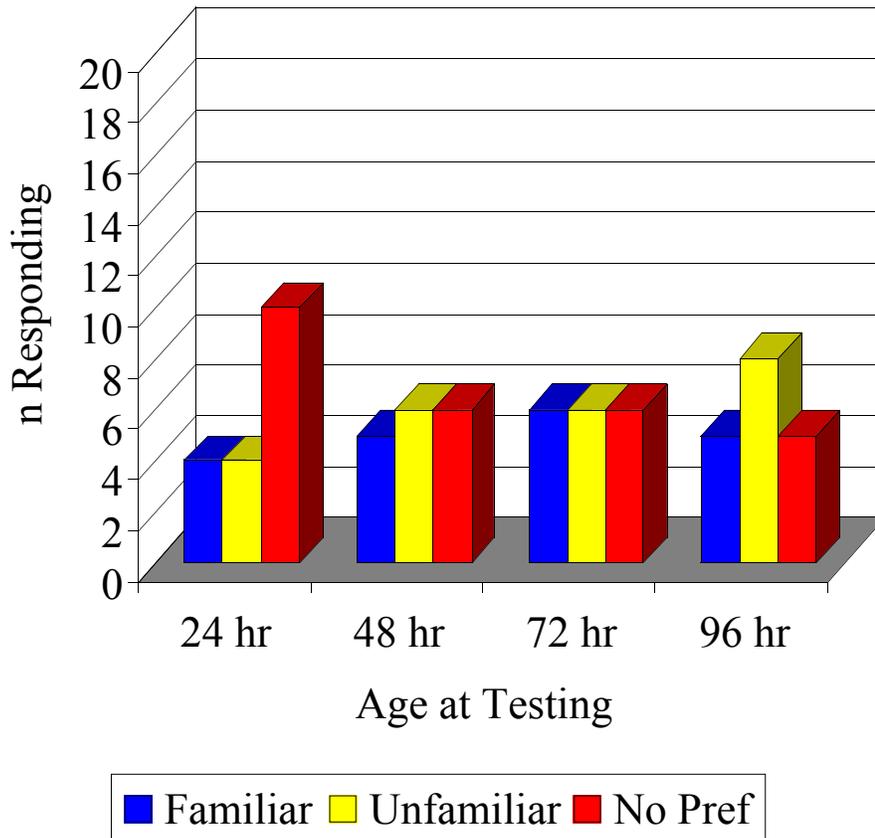
Graph 1. Preference of Chicks in Simultaneous Auditory Choice Tests in Experiment 1A.



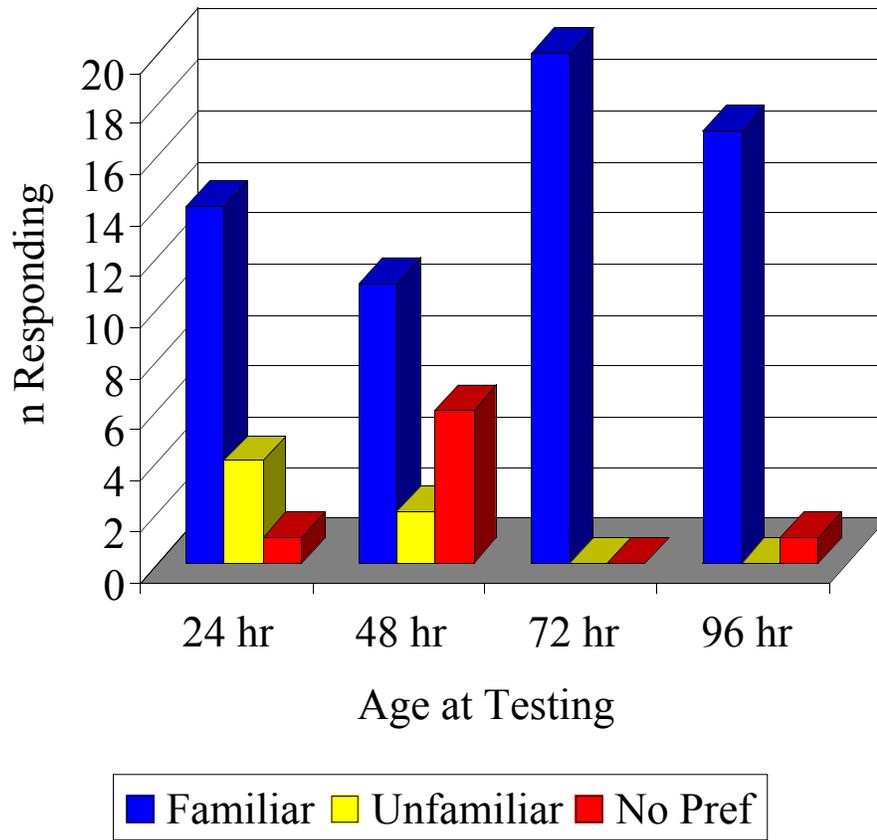
Graph 2. Preference of Chicks in Simultaneous Auditory Choice Tests in Experiment 1B.



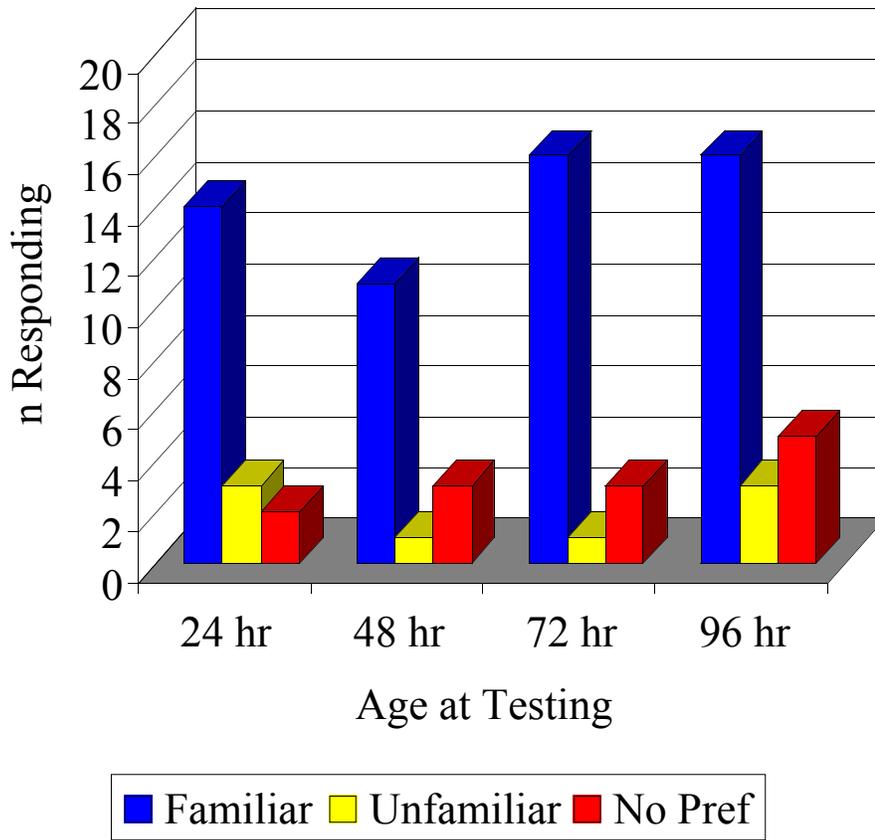
Graph 3. Preference of Chicks in Simultaneous Auditory Choice Tests in Experiment 2.



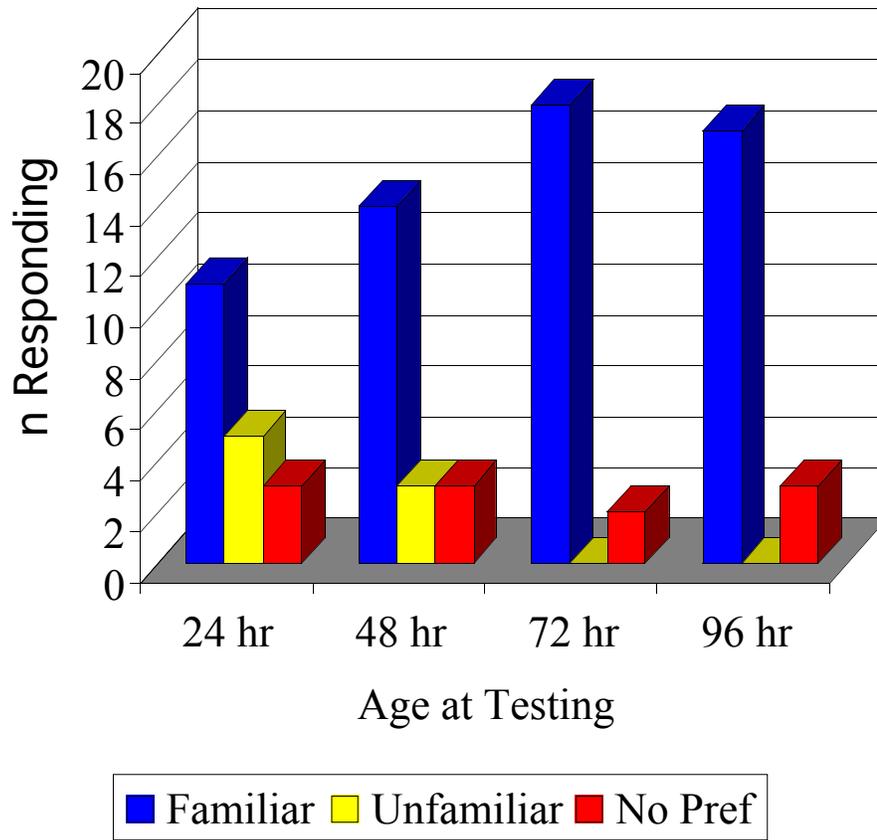
Graph 4. Preference of Chicks in Simultaneous Auditory Choice Tests in Experiment 3A.



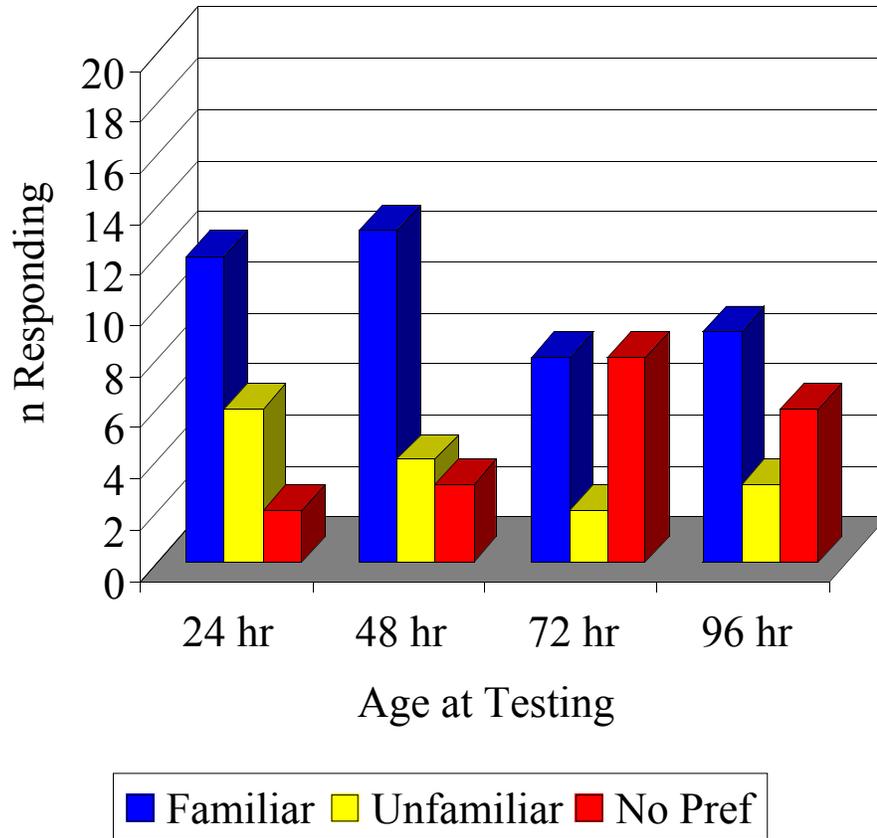
Graph 5. Preference of Chicks in Simultaneous Auditory Choice Tests in Experiment 3B.



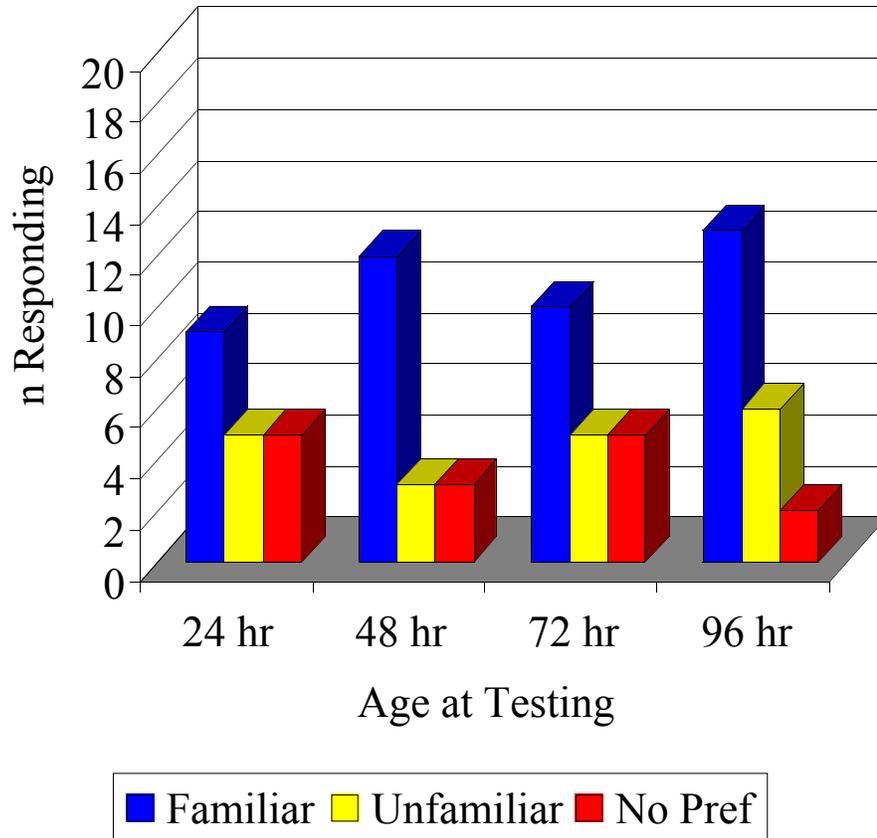
Graph 6. Preference of Chicks in Simultaneous Auditory Choice Tests in Experiment 3C.



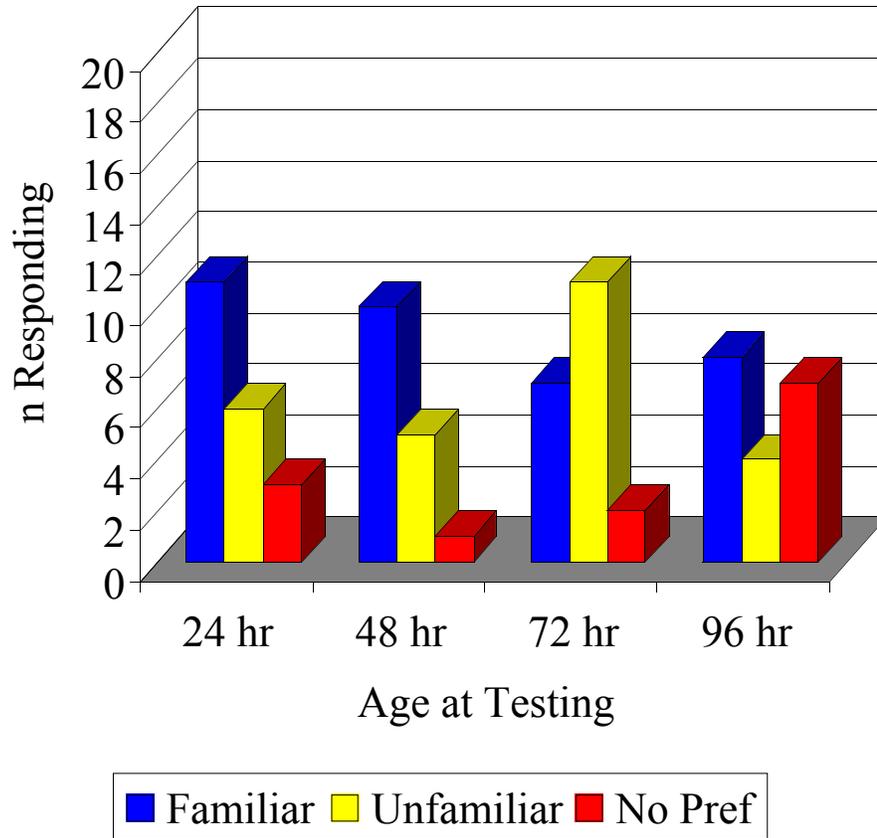
Graph 7. Preference of Chicks in Simultaneous Auditory Choice Tests in Experiment 4A.



Graph 8. Preference of Chicks in Simultaneous Auditory Choice Tests in Experiment 4B.



Graph 9. Preference of Chicks in Simultaneous Auditory Choice Tests in Experiment 4C.



APPENDIX A

Sample Scoring Sheet for Simultaneous Auditory Choice Tests
Used in Experiments 1A-4C.

GROUP: _____ WEEK: _____ SUBJECT: _____

DAY 23: _____ HATCHED: _____ TESTER: _____

TEST 1

DATE: _____ TIME: _____ AGE: _____

STIMULUS A: LATENCY: _____ DURATION: _____

STIMULUS B: LATENCY: _____ DURATION: _____

COMMENTS:

TEST 2

STIMULUS A: LATENCY: _____ DURATION: _____

STIMULUS B: LATENCY: _____ DURATION: _____

COMMENTS:

REBECCA FOUSHEE COLUMBUS

CURRENT ADDRESS:

Department of Psychology

Virginia Polytechnic Institute & State University, Blacksburg, VA 24061-0436

Phone: (540) 231-6581/6398 Email: columbus@vt.edu

EDUCATION:

Ph.D. Developmental Psychology (1998)

Virginia Polytechnic Institute and State University, Blacksburg, VA

Committee Chair: Robert Lickliter, Ph.D.

Dissertation Title:

Auditory-Visual System Interactions: Perinatal Visual Experience Affects
Auditory Learning and Memory in Bobwhite Quail Chicks (Colinus virginianus)

M.S. Developmental Psychology (1996)

Virginia Polytechnic Institute and State University, Blacksburg, VA

Committee Chair: Robert Lickliter, Ph.D.

B.S. Psychology and English Literature (1993)

Summa Cum Laude, Commonwealth Scholar

Virginia Polytechnic Institute and State Univ.

Blacksburg, VA (1991-93)

Randolph-Macon Woman's College

Lynchburg, VA (1989-91)

PROFESSIONAL EXPERIENCE:

Instructor (1997-present)

Virginia Polytechnic Institute & State University, Blacksburg, VA

Courses taught:

- Introductory Psychology
- Developmental Psychology
- Social Psychology
- Advanced Developmental Psychology
- Introductory Psychology Laboratory
- Psychology of Learning

Laboratory Manager (1996-present)

Virginia Polytechnic Institute & State University, Blacksburg, VA

- Managed and maintained NIMH-funded Developmental Psychobiology Research Facility, including equipment purchasing and maintenance, animal care in accordance with federal and state guidelines, personnel management, and laboratory upkeep
- Initiated and coordinated ongoing research projects, including subject procurement, data collection and analysis, and publication of research results
- Trained and supervised team of graduate and undergraduate research assistants in ongoing projects
- Supervised eight undergraduate independent studies and/or undergraduate research projects

Supervisor: Robert Lickliter, Ph.D.

Graduate Research Assistant (1994-96)

Virginia Polytechnic Institute & State University, Blacksburg, VA

- Initiated and conducted experiments on mechanisms of perinatal perceptual organization with bobwhite quail chicks (Colinus virginianus) in NIMH-funded Developmental Psychobiology Research Facility
 - Assisted laboratory manager in daily upkeep of laboratory functions, including undergraduate training, animal care, and coordination of research projects
- Supervisor: Robert Lickliter, Ph.D.

Introductory Psychology Coordinator (1995-96)

Virginia Polytechnic Institute & State University, Blacksburg, VA

- Trained, supervised, and evaluated 23 graduate teaching assistants
- Coordinated 23 GTA's, 2 lecturing faculty, and 1200 undergraduates per semester
- Created syllabi and lesson plans, constructed and analyzed tests, managed departmental research subject pool
- Designed and edited textbook for use in 40 laboratory sections

Supervisor: Jack W. Finney, Ph.D.

PROFESSIONAL MEMBERSHIPS:

American Psychological Association

American Psychological Society

International Society for Developmental Psychobiology

International Society for Infancy Studies

Society for Research in Child Development

PUBLICATIONS (in Refereed Journals):

Columbus, R.F. & Lickliter, R. (1998). Modified postnatal social experience alters the perceptual responsiveness of bobwhite quail chicks (Colinus virginianus). Journal of Comparative Psychology, 112, 161-169.

Columbus, R.F., Sleigh, M.J., Lickliter, R., & Lewkowicz, D.J. (1998). Unimodal sensory experience interferes with responsiveness to the spatial contiguity of multimodal maternal cues. Infant Behavior and Development, 21, 397-409.

Sleigh, M.J., Columbus, R.F., & Lickliter, R. (1998). Intersensory experience and early perceptual development: Postnatal experience with multimodal maternal cues affects intersensory responsiveness in bobwhite quail chicks. Developmental Psychology, 34, 215-223.

Sleigh, M.J., Columbus, R.F., & Lickliter, R. (1996). Type of prenatal sensory experience affects prenatal auditory learning in bobwhite quail (Colinus virginianus). Journal of Comparative Psychology, 110, 233-242.

Lickliter, R., Lewkowicz, D.J., & Columbus, R.F. (1996). Intersensory experience and early perceptual development: The role of spatial contiguity in bobwhite quail chicks' responsiveness to multimodal maternal cues. Developmental Psychobiology, 29, 403-416.

ARTICLES IN PREPARATION:

Columbus, R.F. & Lickliter, R. Attenuated visual stimulation facilitates postnatal auditory learning in bobwhite quail chicks (*Colinus virginianus*).

Columbus, R.F. & Lickliter, R. Sibling interaction facilitates perceptual responsiveness to maternal cues in bobwhite quail chicks.

Columbus, R.F., Roberts, J., & Lickliter, R. Type of prenatal auditory stimulation affects heart rate in bobwhite quail embryos.

Masaniello, S., Columbus, R.F., & Lickliter, R. Type and amount of postnatal visual stimulation affects intersensory development of bobwhite quail chicks.

Columbus, R.F., Ward, G.M., & Lickliter, R. Perinatal auditory stimulation affects visual responsiveness in bobwhite quail chicks.

PAPERS PRESENTED AT SCIENTIFIC MEETINGS:

Columbus, R.F. & Lickliter, R. Postnatal social experience facilitates species-typical maternal preferences in bobwhite quail chicks. Presented at the American Psychological Society 10th Annual Convention, Washington, DC, May 1998.

Columbus, R.F. & Lickliter, R. Early experience and auditory learning: The role of sensory stimulation in bobwhite quail chicks' preferences for maternal cues. Presented at the International Conference for Infant Studies, Atlanta, GA, April 1998.

Columbus, R.F. & Lickliter, R. Attenuated visual stimulation facilitates postnatal auditory learning in bobwhite quail chicks (*Colinus virginianus*). Presented at the International Society for Developmental Psychobiology Annual Meeting, New Orleans, LA, October, 1997.

Lickliter, R., Bahrick, L., Columbus, R.F. & Sleigh, M.J. Augmented unimodal sensory experience alters perceptual responsiveness to maternal cues in bobwhite quail chicks. Presented at the International Society for Developmental Psychobiology Annual Meeting, New Orleans, LA, October, 1997.

Columbus, R.F. & Lickliter, R. Sibling interaction facilitates perceptual responsiveness to maternal cues in bobwhite quail chicks. Presented at the American Psychological Society 9th Annual Convention, Washington, DC, May 1997.

Columbus, R.F., Sleigh, M.J., Lickliter, R., & Lewkowicz, D.J. The role of temporal contiguity in bobwhite quail chicks' responsiveness to spatial features of multimodal maternal cues. Presented at the Eastern Psychological Association Annual Meeting, Washington, DC, April, 1997.

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

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

Sleight, 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., Sleight, 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.

BOOKS (Edited):

Sleight, M.J., Columbus, R.F., & Sgro, J.A. (1996). Exploring introductory psychology. New York: McGraw-Hill.

HONORS AND AWARDS

Extramural Awards:

- Frank A Beach Comparative Psychology Award (August 1997)
 - Division 6: Behavioral Neuroscience and Comparative Psychology, American Psychological Association
- Sandra G. Wiener Developmental Psychobiology Student Investigator Award, International Society for Developmental Psychobiology (November, 1996)
- *Phi Beta Kappa, Phi Kappa Phi, Psi Chi*

Intramural Awards:

- VPI & SU Graduate Student Travel Fund Award (January, 1998)
- First Place, Graduate Student Research Symposium, VPI & SU (April 1997)
- VPI & SU Graduate Student Travel Fund Award (August, 1995)

GRANTS:

- VPI & SU Graduate Student Assembly Organization Travel Grant, April 1998
- VPI & SU Graduate Research Development Grant (PI), February 1996

PROFESSIONAL SERVICE:

Secretary, Developmental Science Society (1997-present), VPI & SU, Blacksburg, VA
Investigator, Graduate Student Honor System (1997-98), VPI & SU, Blacksburg, VA
Representative, Graduate Student Honor System (1996-97), VPI & SU, Blacksburg, VA

WORKSHOP PRESENTATIONS:

Columbus, R.F. (August 1998). Qualitative Grading Tips: Effective Techniques for Accurate, Objective, and Consistent Grading. Graduate Teaching Assistant Training Workshop, Virginia Polytechnic Institute and State University, Blacksburg, VA.

WORKSHOPS ATTENDED:

- NSF/NIMH/NIH APS Workshop on Writing Research Grant Proposals. (May 1998). American Psychological Society 10th Annual Convention, Washington, DC.
- Training the Future Professoriate. (March, 1997). Virginia Polytechnic Institute and State University, Blacksburg, VA.

UNDERGRADUATE RESEARCH PROJECTS / INDEPENDENT STUDIES**SUPERVISED:**Research Projects:

Sharon Masaniello. Spring 1998. Altered postnatal visual experience affects intersensory development in bobwhite quail chicks. Senior Honors Thesis Project.

Rhonda Quesenberry. Spring 1998. Altered auditory experience affects intersensory development in bobwhite quail chicks. Senior Research Project.

Kelly A. Ryan. Spring 1996. Social interaction and perinatal perceptual development in bobwhite quail chicks. Senior Research Project.

Independent Study Projects:

Gina Ward. Fall 1998. Dynamic systems in development. Independent Study.

Summer Alis Jennings. Spring 1998. Avian perinatal perceptual development. Independent Study.

Sharon Masaniello. Fall 1997. Visual perception in bobwhite quail chicks. Honors Independent Study.

Rhonda Quesenberry. Fall 1997. Auditory perceptual development in bobwhite quail chicks. Independent Study.

Sharon Masaniello. Spring 1996. Perceptual development of bobwhite quail chicks. Independent Study.

RESEARCH & THEORETICAL INTERESTS:

- Psychobiological, Behavioral, and Social Determinants of Learning and Memory
- Role of Early Experience in Learning and Developmental Outcomes
- Behavioral State Regulation and Sensory System Organization in Early Development
- Contextual Determinants of Psychobiological Organization During Prenatal and Postnatal Development
- Developmental Psychobiological Perspective of Learning, Ecological and Perceptual Learning Theory, History of Psychology, Future Directions in Developmental Theory and Research
- Dynamical Systems Approach to Studying Learning and Development