

Intersensory Experience and Early Perceptual Development: Attenuated Prenatal Sensory Stimulation Affects Postnatal Auditory and Visual Responsiveness in Bobwhite Quail Chicks (*Colinus virginianus*)

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Related experiments examined the effects of attenuated prenatal sensory stimulation on subsequent postnatal auditory and visual responsiveness in precocial bobwhite quail chicks (*Colinus virginianus*). Results revealed that denying quail embryos the prenatal vestibular and tactile stimulation provided by broodmates during incubation alters pre- and postnatal perceptual functioning. Chicks incubated in physical isolation during the late stages of prenatal development responded to maternal auditory cues into later stages of the postnatal period and failed to respond to maternal visual cues at ages communally incubated chicks typically display such visual responsiveness. In addition, embryos incubated in physical isolation failed to exhibit early auditory learning of an individual maternal call, a behavior reliably seen in communally incubated embryos. Taken together, these results and those from related studies indicate that a substantial decrease or increase in the range of sensory stimulation normally present in the prenatal period can result in a slowing of the rate of species-specific perceptual development and suggest that some optimal range of prenatal sensory stimulation is necessary for species-typical perceptual capacities to emerge.

The prenatal environment of avian and mammalian species is rich in tactile, vestibular, chemical, and auditory sensory stimulation (Freeman & Vince, 1974; Ronca, Lamkin, & Alberts, 1993; Smotherman & Robinson, 1986). In many species, the sensory systems capable of responding to these types of inputs are already well developed and functional before birth or hatching (Alberts, 1984; Bradley & Mistretta, 1975; Gottlieb, 1971). The availability of a rich sensory environment during the prenatal period, coupled with the embryo or fetus's capacity to respond to it, suggests that the development of early perceptual organization may be strongly influenced by prenatal sensory experience. In this light, several studies have shown that the human fetus is sensitive and responsive to auditory stimulation and can retain the effects of prenatal auditory experience into postnatal life (DeCasper & Spence, 1991; Fifer & Moon, 1988). Studies with both infrahuman mammalian species and human fetuses have also shown that prenatal experience with chemosensory stimulation can exert significant effects on subsequent postnatal behavior. For example, Smotherman and

Robinson (1987) demonstrated that rat fetuses exhibit a form of olfactory sensitization that has long-lasting effects on postnatal suckling and consummatory behaviors. Marlier, Schaal, and Soussignan (1994) showed that human neonates prefer the smell of amniotic fluid over distilled water, suggesting that experience with the prenatal chemical environment has consequences for the postnatal functional organization of the olfactory system.

A potentially important feature of prenatal sensory experience is that it can be multisensory in nature. That is, a mammalian fetus or avian embryo may experience sensory stimulation of the vestibular, somesthetic, chemical, or auditory modalities simultaneously or sequentially. This condition raises the interesting possibility that prenatal stimulative effects in one sensory modality may have lasting effects on responsiveness to stimulation in other modalities. Recent work with a variety of animal species has demonstrated such effects of modified perinatal sensory experience in one modality on subsequent postnatal perceptual organization (Banker & Lickliter, 1993; Foreman & Altaha, 1991; Gottlieb, 1993; Gottlieb, Tomlinson, & Radell, 1989; Kenny & Turkewitz, 1986; Lickliter, 1990a, 1990b, 1994; Lickliter & Stoumbos, 1991; Radell & Gottlieb, 1992; Symons & Tees, 1990) and has raised a number of questions regarding the particular aspects of perinatal sensory stimulation that can mediate change in early intersensory relationships. For example, several recent studies using animal embryos and infants have demonstrated that specific experiential manipulations of perinatal sensory stimulation can either result in the facilitation of early intersensory responsiveness (Lickliter, 1990a, 1994; Symons & Tees, 1990) or interfere with early intersensory capacities (Kenny & Turkewitz, 1986; McBride & Lickliter, 1994). What remains unclear at present is why sensory augmentation or deprivation procedures can result in the facilitation of intersensory integration in some studies and disruptive effects on intersensory integration in others.

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Although the effects that altered perinatal sensory experience may have on subsequent perceptual organization is likely to depend on a number of nested factors, including the timing of the manipulation in relation to the developmental stage of the infant (Gottlieb, 1971; Turkewitz & Kenny, 1982) and the type of stimulation provided or denied (Gottlieb, 1981, 1991a; McBride & Lickliter, 1994), several recent studies using precocial birds have also indicated that the overall amount of sensory stimulation present in the perinatal environment can have a significant influence on the embryo or neonate's sensitivity to specific sensory input (Gottlieb, 1991b, 1993; Gray, 1990; McBride & Lickliter, 1993). In particular, these studies suggest that the amount of sensory stimulation provided by social experience with broodmates in the period immediately following hatching can affect the arousal level of hatchlings and thereby serve to either increase (Gottlieb, 1993; McBride & Lickliter, 1993) or decrease (McBride & Lickliter, 1994) chicks' sensitivity to specific auditory or visual stimulation present in the postnatal environment. For example, a recent study using ducklings (Gottlieb, 1993) found that tactile stimulation afforded by normal social interaction with broodmates is essential for postnatal auditory learning of a nonmaternal call; ducklings reared in tactile isolation from conspecifics did not exhibit the usual postnatal auditory-learning abilities seen in group-reared birds. Gottlieb (1993) reasoned that tactile isolation deprives hatchlings of normal levels of perinatal sensory stimulation and thereby engenders a high level of arousal in hatchlings. This high level of arousal (assessed by number of distress vocalizations emitted by subjects) appears to disrupt the young duckling's attentional capacity for the experimental auditory stimulus and thus serves to interfere with typical patterns of early auditory learning.

To further examine this notion of optimal levels or thresholds of sensory stimulation as it applies to the prenatal period of development, we designed the present study to determine whether attenuating the amount of sensory stimulation normally present in the prenatal environment would affect subsequent perceptual functioning in bobwhite quail chicks. Specifically, in light of previous research with precocial avian hatchlings (see Lickliter, Dyer, & McBride, 1993, for a review), we predicted that avian embryos denied the normally occurring vestibular and tactile stimulation typically provided to them by broodmates during the late stages of the prenatal period would likely demonstrate patterns of perceptual organization different from embryos allowed unrestricted physical stimulation from their broodmates. Specifically, we reasoned that because of their substantially reduced levels of normally occurring prenatal sensory stimulation, embryos incubated in physical isolation from conspecifics would show functional deficits in their subsequent auditory and visual responsiveness to species-specific maternal cues.

General Method

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

Subjects

Three hundred and sixty-one incubator-reared bobwhite quail chicks (*Colinus virginianus*) were used as subjects. Fertile, unincubated eggs were received weekly from a commercial supplier and were set in a Petersime Model I incubator, maintained at 37.5 °C and 85%–90% relative

humidity. After 20 days of incubation, the eggs were transferred to a hatching tray located at 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. Chicks that hatched earlier or later than this 24-hr window were excluded from the various experiments. 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. This restriction in developmental age consistently excluded approximately 20% of the chicks from any given batch (week) of eggs. The possible influence of between-batches variation in behavior was controlled by drawing subjects for each experimental group from three or more different batches (i.e., weeks) of eggs. As a result of their incubator rearing, the only sounds to which embryos and hatchlings were exposed until the time of experimental manipulation or testing were their own embryonic and postnatal vocalizations (and those of their broodmates) and the low-frequency background noises emanating from the incubator fan and motor. Following hatching, subjects were group-reared in large plastic tubs (45 × 25 × 15 cm) containing 10–12 same-age chicks to mimic naturally occurring brood conditions (Stokes, 1967). The sound-attenuated room in which the hatchlings were kept 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 were continuously available throughout the duration of each experiment.

Procedure

To ensure that the embryos could hear or see the sensory stimulation presented in the various experiments in the period before hatching, during the second half of the 21st day of incubation, we removed a portion (approximately 1.5 cm in diameter) of the shell and inner-shell membrane over the air space of the egg of each subject. The embryo's bill usually penetrates the air space at the large end of the egg early on day 21, and at this time the embryo begins to respire and vocalize (Freeman & Vince, 1974). As a result, removing the top portion of the shell (the embryo's postural orientation is not altered and the head and body remain confined in the shell) does not affect incubation, survivability, or species-typical perceptual behavior (Lickliter, 1990b; Lickliter & Stoumbos, 1991). Following the egg-opening procedure, each embryo (still confined within its egg) was placed in an individual, opaque plastic tub (7 cm³) and was incubated in a portable incubator for the last 24–36 hr of incubation. Each portable incubator contained 12 of these isolation tubs; embryos were thus able to hear but not physically contact other broodmates during the late stages of incubation. Temperature and humidity were maintained as during earlier incubation.

Testing

Testing took place 24, 48, or 72 hr (±3 hr) after hatching. Each chick was tested only once. The testing apparatus was located in a sound-attenuated room and consisted of a large circular arena, 160 cm in diameter, surrounded by a black curtain that 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 × 15 cm) were delineated on opposite sides of the arena by green lines painted on the floor. These approach areas constituted less than 5% of the total area of the arena, so preference scores were based on strict criteria. To begin a preference test, we placed each chick at a start point equidistant from the two approach areas. A mid-range dome-radiator speaker was positioned behind the curtain in each of the approach areas, and each speaker was connected to its own cassette tape player located at a control table. An observer who was unaware of each experiment's design sat at this table and observed each

chick's activity through a large mirror positioned above the arena. The testing room were maintained at approximately 26 °C throughout the study.

All of the birds were tested individually in a 5-min simultaneous choice test and were scored on both the latency of approach and duration of time spent in each of the two approach areas. Depending on the particular experiment, each chick was tested for its preference between either two auditory stimuli or two audiovisual stimuli presented on either side of the arena. The location of the auditory and visual stimuli presented during testing in each experiment was alternated between chicks to prevent any possible side bias from influencing results. Latency was scored as the amount of time (in seconds) elapsed from the onset of the trial until the subject entered an approach area. Duration was scored as the cumulative amount of time (in seconds) the bird 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 was recorded. Occasionally, a bird entered both 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 consecutive seconds for a duration score to be counted; this criterion prevented any random movements from being counted as a response to the presented stimuli. If a subject did not move from the start point during the test trial, it was considered a nonresponder and received a score of 300 s for latency (the length of the trial) and 0 s for duration for both test stimuli.

Data Analysis

The primary data of interest in each experiment were the measures of preference (derived from latency and duration of response) for the auditory and visual stimuli presented during the trials. Two such measures of preference were used: (a) Differences in the latency of approach to each stimulus by a subject in a group was evaluated by the Wilcoxon matched-pairs signed-ranks test, and (b) an individual preference, derived from duration of time spent in proximity to each stimulus, was assigned to any subject that stayed in one area for more than twice as long as the other; this measure was evaluated by the chi-square test. Preliminary analyses of these two measures indicated that they were perfectly correlated, so to reduce redundancy, we did not present latency measures in any detail. Significance levels set at $p < .05$ were used to evaluate results, and all reported p values are two-tailed.

Experiment 1: Effects of Attenuated Prenatal Sensory Stimulation on Postnatal Auditory Responsiveness

Previous studies have demonstrated that at 24 hr and 48 hr following hatching, bobwhite quail chicks can direct their social preferences solely on the basis of available maternal auditory cues (Heaton, Miller, & Goodwin, 1978; Lickliter, 1994; Lickliter & Virkar, 1989). By 72 hr of age, chicks require combined maternal auditory and visual stimulation to direct their social preferences (Lickliter & Virkar, 1989; McBride & Lickliter, 1994). In contrast, chicks exposed to unusually early visual experience as embryos do not exhibit a preference for the bobwhite maternal call at either 24 hr or 48 hr following hatching (Lickliter, 1990b). Rather, these chicks require both maternal auditory and visual cues to direct their preferential responsiveness by 24 hr following hatching (Lickliter, 1990a, 1990b). This finding suggests that augmented prenatal visual stimulation serves to accelerate the developmental emergence of intersensory integration that under normal circumstances does not

appear until 72 hr following hatching (see Lickliter & Banker, 1994, for a more detailed discussion).

The specific mechanism that mediates the acceleration of intersensory integration following unusually early visual experience is presently unknown. However, the unusually early visual stimulation presented to embryos in the Lickliter (1990a, 1990b) studies was given to communally incubated embryos. As a result, these embryos were exposed to a variety of sensory stimuli from broodmates in addition to prenatal visual stimulation. These various stimuli included the vestibular and tactile stimulation provided by broodmates during the hatching process as emerging hatchlings roll into, push against, and climb over other eggs of their clutch. It is possible that this "background" sensory stimulation provided by broodmates during the late stages of incubation is essential in maintaining the embryos' overall level of arousal in a range that is optimal for attending and responding to the premature visual stimulation. As a first step in examining this possibility, in the present experiment, we deprived one group of bobwhite embryos of normally occurring physical contact with broodmates during the last stages of incubation to determine whether the absence of such sensory experience plays a role in their subsequent perceptual functioning. A second group of bobwhite embryos was also deprived of normally occurring vestibular and tactile stimulation from broodmates and in addition received visual stimulation before hatching. If the background level of stimulation provided by physical contact with broodmates is essential to the facilitation of embryos' responsiveness to earlier-than-usual visual input, then embryos deprived of such stimulation should exhibit patterns of responsiveness different from those previously observed in communally incubated chicks.

Method

One hundred and twenty bobwhite quail chicks, drawn from 11 separate hatches, served as subjects. Subjects were divided into an isolation group ($n = 64$) and an isolation-visual stimulation group ($n = 56$). Chicks in the isolation group underwent the egg-opening procedure on the second half of day 21, as described in the General Method section, and were then incubated to hatching in isolation tubs placed in a group of 12 in a portable incubator located in a darkened room. These subjects received attenuated sensory stimulation from broodmates during the last 24–36 hr before hatching, in that they could hear other embryos in the incubator but could not physically contact these embryos. Because of their lack of physical contact with broodmates, embryos were denied the vestibular and tactile stimulation typically provided to them by broodmates during the hatching process. Chicks in the isolation-visual stimulation group underwent the same egg-opening procedure and were then incubated to hatching in isolation tubs while being exposed to a 15-W light pulsed at 3 cycles per second (maximum flash energy = 4-W s) for 10 min each hour. This temporally patterned light was located immediately above the Plexiglas top of the incubator, and particular care was taken to ensure that the presence of the light did not alter the ambient air temperature or relative humidity within the incubator. Embryos in this group thus received attenuated sensory stimulation from broodmates and unusually early visual stimulation for 10 min each hour during the last 24 to 36 hr before hatching. Although the precocial avian embryo is responsive to prenatal visual stimulation (Heaton, 1973; Oppenheim, 1968), the embryo does not ordinarily experience patterned visual stimulation until after hatching from the egg.

Following hatching, all chicks from both groups were reared socially in groups of 10–12 same-age chicks, in which they remained until testing at

24, 48, or 72 hr of postnatal age. Testing consisted of presenting subjects with a simultaneous choice test between the bobwhite maternal call and a chicken maternal call (see Heaton et al., 1978, for acoustical details). Choice, latency, and duration of response were scored as described in the General Method section.

Results and Discussion

The results of this experiment are illustrated in Table 1. Birds in both the isolation group and the isolation-visual stimulation group exhibited a significant preference for the bobwhite maternal call over the chicken maternal call at 24, 48, and 72 hr following hatching ($p < .001$). The analysis of the latency scores further supported these findings: At all ages tested, both groups showed shorter latencies in their response to the bobwhite maternal call over the chicken maternal call ($p < .01$).

These findings stand in contrast to the results obtained from communally incubated chicks in previous studies (Banker & Lickliter, 1993; Lickliter, 1990a, 1990b, 1994; Lickliter & Virkar, 1989). In these studies, normally reared chicks consistently preferred the bobwhite maternal call over the chicken maternal call at 24 hr and 48 hr following hatching, but not at 72 hr. In addition, communally incubated chicks who received unusually early (prenatal) visual experience as embryos did not prefer the bobwhite maternal call presented without maternal visual cues at 24, 48, or 72 hr following hatching (Lickliter, 1990a, 1990b). In the present experiment, chicks incubated in isolation (isolation group) and chicks incubated in isolation and exposed to unusually early visual experience (isolation-visual stimulation group) demonstrated an auditory preference for the bobwhite maternal call into later stages of postnatal development than seen in communally incubated chicks. Specifically, chicks in both groups continued to respond preferentially to the bobwhite maternal call through 72 hr of age, whether or not they had received unusually early visual stimulation as embryos.

The fact that chicks incubated in isolation and exposed to prenatal visual experience continued to respond to maternal auditory cues at 72 hr is particularly striking, in that these chicks responded to the maternal call some 3 days later into postnatal development than communally incubated chicks re-

ceiving prenatal visual stimulation (Lickliter, 1990a). It appears that elimination of the normally available sensory stimulation were from broodmates during the late stages of incubation alters the embryo's sensitivity to the presentation of prenatal visual stimulation, in that chicks receiving unusually early visual experience showed the same pattern of responsiveness to the maternal call as chicks not receiving visual experience as embryos (Table 1). What is not clear from the present results, however, is how general this effect is. If the sensory stimulation provided by broodmates under normal incubation conditions serves to provide a level of stimulation necessary for responding to unusually early visual stimulation, then the effects found in the present experiment should generalize to responsiveness in other sensory systems. The purpose of the next experiment was to investigate this possibility by assessing the effects of isolation and prenatal visual stimulation on chicks' postnatal visual, rather than auditory, responsiveness to maternal cues.

Experiment 2: Effects of Attenuated Prenatal Sensory Stimulation on Postnatal Visual Responsiveness

Previous research has revealed that normally reared, communally incubated bobwhite quail chicks show a significant visual preference for a bobwhite hen model over a scaled quail hen model when both are emitting the same bobwhite maternal call by 72 hr following hatching (but not at earlier ages; Lickliter, 1994; Lickliter & Virkar, 1989; McBride & Lickliter, 1993). In contrast, communally incubated chicks who received prenatal visual experience as embryos demonstrate a preference for the bobwhite hen over the scaled quail hen (when both are emitting the same bobwhite maternal call) by 24 hr following hatching (Lickliter, 1990a). It is important to note that the static visual cues provided by the hen models alone are not sufficient to elicit preferential responsiveness at any of the ages tested. Rather, maternal visual cues must be presented with the maternal call to be effective in directing social preferences (Lickliter, 1994; Lickliter & Virkar, 1989).

The present experiment was designed to examine the influence of prenatal sensory stimulation from broodmates on chicks' postnatal visual responsiveness to maternal cues. If the

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

Group/age	n	n responding	Preference		
			Bobwhite maternal call	Chicken maternal call	No preference
Isolation					
24 hr	23	19	19*	0	0
48 hr	22	18	18*	0	0
72 hr	19	16	16*	0	0
Isolation-visual stimulation					
24 hr	19	15	14*	0	1
48 hr	18	14	13*	1	0
72 hr	19	14	14*	0	0

* $p < .001$ (chi-square test).

lack of normally present sensory stimulation from broodmates makes it more difficult for embryos to attend or respond to unusually early visual stimulation, then chicks incubated in physical isolation from broodmates should not demonstrate the postnatal acceleration of the emergence of intersensory integration previously observed in communally incubated chicks exposed to prenatal visual stimulation during the late stages of incubation.

Method

A total of 141 bobwhite quail chicks, drawn from 15 separate hatches, served as subjects. Experimental chicks were divided into an isolation group ($n = 62$) and an isolation-visual stimulation group ($n = 59$) and received the same prenatal procedures as subjects in the previous experiment. Control chicks ($n = 20$) were communally incubated and received the same prenatal visual stimulation described in Experiment 1. Following hatching, all chicks were reared socially in groups of 10-12 same-age chicks and were tested individually at 24, 48, or 72 hr of postnatal age. Testing consisted of presenting hatchlings with a simultaneous choice test between the bobwhite maternal call paired with either a stuffed adult bobwhite hen or a stuffed scaled quail hen (for a photo of these stimuli, see Banker & Lickliter, 1993, Figure 1). In other words, during testing, both hen models were emitting the same species-typical bobwhite maternal call, requiring subjects to direct their social preference on the basis of available visual cues. Choice, latency, and duration of response were scored as described in the General Method section.

Results and Discussion

The results of testing are shown in Table 2. Experimental chicks in both the isolation group and the isolation-visual stimulation group did not show a preference for either the bobwhite hen model paired with the bobwhite maternal call or the scaled quail hen model paired with the bobwhite maternal call at any of the ages tested. Correspondingly, there were no significant differences in latency scores for either stimulus array in either experimental group at 24, 48, or 72 hr following hatching.

These results differ markedly from the results obtained from the communally incubated and visually stimulated control chicks, which preferred the bobwhite hen over the scaled quail

hen by 24 hr following hatching (see Table 2; see also Lickliter, 1990a). In addition, the results from experimental chicks in this study differed from the results of communally incubated chicks in previous studies, which did not receive unusually early visual stimulation (Banker & Lickliter, 1993; Lickliter, 1990a, 1990b; Lickliter & Virkar, 1989; McBride & Lickliter, 1993). In these studies, normally reared, unmanipulated chicks consistently preferred the bobwhite hen paired with the bobwhite maternal call over the scaled quail hen paired with the bobwhite maternal call by 72 hr following hatching. In the present experiment, chicks incubated in isolation (isolation group) and chicks incubated in isolation and exposed to unusually early visual experience (isolation-visual stimulation group) did not prefer the bobwhite hen by 72 hr of age, indicating that the onset of chicks' visual responsiveness to maternal cues is compromised as a result of attenuated prenatal stimulation. These findings further support the notion that physical isolation from broodmates somehow alters the embryo's sensitivity to the augmented visual stimulation present in the period before hatching. If this pattern is generalizable to other modalities, then embryos' sensitivity to augmented auditory stimulation should also be adversely affected under conditions of attenuated prenatal sensory stimulation. The purpose of the next experiment was to examine this possibility.

Experiment 3: Effects of Attenuated Prenatal Sensory Stimulation on Auditory Learning

Previous research has shown that communally incubated bobwhite quail embryos can learn an individual bobwhite maternal call and remember that familiar call for at least 24 hr after exposure. Specifically, embryos exposed to a particular variant of the bobwhite maternal call during the later stages of incubation subsequently demonstrate an auditory preference for that call over another bobwhite maternal call when tested postnatally (Lickliter & Hellewell, 1992). To further investigate the impact of prenatal stimulation from broodmates on early perceptual functioning, this experiment assessed auditory learning in

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

Group/age	n	n responding	Preference		
			Bobwhite call & bobwhite hen	Bobwhite call & scaled hen	No preference
<i>Isolation-no stimulation</i>					
24 hr	20	17	9	6	2
48 hr	21	16	6	8	2
72 hr	21	16	5	7	4
<i>Isolation-visual stimulation</i>					
24 hr	20	16	4	5	7
48 hr	21	19	8	5	6
72 hr	18	13	5	3	5
<i>Communal-visual stimulation (controls)</i>					
24 hr	20	17	13*	2	2

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

bobwhite embryos denied physical contact with broodmates during the later stages of incubation.

Method

Sixty bobwhite quail embryos, drawn from seven separate hatches, served as subjects. The embryos were divided into a control group ($n = 20$), an isolation–no-exposure group ($n = 20$), and an isolation–exposure group ($n = 20$). Experimental embryos in the isolation–no-exposure group underwent the egg-opening procedure as in the previous experiments and were then incubated to hatching in isolation tubs in a portable incubator located in a darkened room. Experimental embryos in the isolation–exposure group underwent the egg-opening procedure and were then incubated in isolation tubs in a darkened room while being exposed to an individual bobwhite maternal call (Call B) for 10 min each hour for 24 hr before hatching. Control embryos underwent the egg-opening procedure and were then communally incubated in a darkened room while being exposed to bobwhite maternal Call B. Auditory stimulation commenced on the second half of the 21st day of incubation and continued through the second half of the 22nd day of incubation. Total prenatal auditory stimulation with the maternal call thus amounted to approximately 4 hr for the isolation–exposure group and the communal control group. The recording of the individual maternal call was played to the embryos through a Marantz Model PMD 221 cassette recorder and presented at a peak intensity of 65 dB, as measured by a Bruel & Kjaer Model 2232 sound-level meter. All the normally occurring acoustic components of the maternal vocalization were present and unaltered. After hatching, all subjects were reared socially with 10 to 12 same-age chicks until testing at 24 hr of postnatal age. During testing, individual subjects were given a simultaneous choice test between the familiar bobwhite maternal call (Call B) and an unfamiliar variant of the bobwhite maternal call (Call A). These two maternal calls were recorded in the field and were similar in phrasing, call duration, repetition rate, dominant frequency, and frequency modulation (see Table 1 in Heaton et al., 1978). The sound intensity of both of the calls peaked at 65 dB at the point in which the chick was introduced into the test arena. Choice, latency, and duration of response was scored as described in the General Method section.

Results and Discussion

As shown in Table 3, the two variants of the bobwhite maternal call were equally attractive to the isolation–no-exposure chicks at 24 hr following hatching. Birds which demonstrated a preference from this group (i.e., spent twice as long in one approach area as the

other) were just as likely to prefer Call A (the unfamiliar call) as Call B (the familiar call) in the simultaneous choice test. Analysis of the latency of response also revealed no preference between the two bobwhite maternal calls. Experimental chicks exposed to Call B as isolated embryos (isolation–exposure group) likewise did not demonstrate a preference for either of the two maternal calls at 24 hr following hatching. The analysis of latency scores by the Wilcoxon test further supported this finding: Scores were not significantly different between the familiar and unfamiliar auditory stimuli presented during testing. In contrast, communally incubated chicks in the control group demonstrated a significant preference for the familiar maternal Call B at 24 hr following hatching. Analysis of latency scores also revealed a preference for the familiar maternal call, with chicks showing shorter latencies in their response to the familiar Call B than to the unfamiliar Call A ($p < .01$).

These results from the control chicks parallel the results obtained from communally incubated embryos in a previous study (Lickliter & Hellewell, 1992). In that study, chicks that had been incubated communally and exposed to Call B as embryos also preferred the familiar maternal call over the unfamiliar call variant at 24 hr following hatching. The fact that the experimental chicks in the isolation–exposure group in the present experiment did not learn the individual maternal call as embryos further supports our prediction that the lack of background sensory stimulation provided by broodmates leads to an insensitivity to the effects of specific prenatal experience. The results of this experiment, combined with those from Experiments 1 and 2, demonstrate the generality of this insensitivity phenomenon and suggest the possibility of a general arousal-based mechanism. This arousal-based mechanism is presumed to be regulated by some optimal level of overall sensory stimulation (typically provided by the vestibular, tactile, and proprioceptive experience associated with the late stages of incubation), which makes it possible for the embryo to attend and respond to additional sensory experience present in the prenatal environment.

Experiment 4: Effects of Concurrent Prenatal Isolation and Visual Stimulation on Auditory Learning

A recent study using duck embryos and hatchlings found that embryos receiving substantially increased amounts of prenatal vestibular, tactile, and proprioceptive stimulation fail to learn an individual duck maternal call (Radell & Gottlieb, 1992),

Table 3
Preference of Chicks in Simultaneous Auditory Choice Tests at 24 Hours Following Hatching in Experiments 3 and 4

Group	n	n responding	Preference		
			Bobwhite Call A (unfamiliar)	Bobwhite Call B (familiar)	No preference
Isolation–no exposure	20	19	8	6	5
Isolation–exposure	20	19	7	6	6
Communal–exposure (controls)	20	20	3	14*	3
Isolation–concurrent auditory + visual group	20	19	5	13*	1

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

whereas duck embryos receiving no augmented stimulation or only slightly augmented amounts of stimulation demonstrate a postnatal preference for the familiar individual duck maternal call (Gottlieb, Tomlinson, & Radell, 1989; Radell & Gottlieb, 1992). We obtained a similar failure to learn an individual maternal call in Experiment 3, but in our case this result was obtained in embryos that received decreased amounts of prenatal vestibular, tactile, and proprioceptive stimulation as a result of their isolation from broodmates during the late stages of incubation. This finding suggests that some optimal level of overall sensory stimulation is required for the development of normal or species-typical perceptual capacity. In other words, it appears that any substantial deviation from the range of sensory stimulation normally encountered prenatally (be it more or less than normal) is likely to result in altered patterns of perceptual functioning.

If the range of stimulation hypothesis that we have proposed to account for the results from the previous three experiments is correct, then it should be possible to obtain prenatal learning of an individual maternal call by providing increased sensory stimulation to physically isolated embryos during exposure to the call. The purpose of the final experiment was to examine this possibility by repeating the procedures of Experiment 3, except that this time in addition to being exposed to a specific maternal call before hatching, isolated embryos also were exposed to concurrent visual stimulation. We predicted that if a substantial reduction in the amount of overall sensory stimulation normally present in the prenatal environment was responsible for the functional deficit seen in the prior experiment, then increasing the amount of sensory stimulation (regardless of the specific type of stimulation) available to the embryo during exposure to the maternal call should provide an adequate level or threshold of stimulation to facilitate prenatal auditory learning.

Method

Twenty bobwhite quail embryos, drawn from three separate hatches, served as subjects. The experimental procedures of Experiment 3 were repeated, except that in this experiment subjects also received exposure to a temporally patterned light during their exposure to the individual maternal call. Specifically, embryos incubated in isolation were exposed to a 15-W light pulsed at three cycles per second during the 10 min/hr that the maternal call was broadcast. Subjects thus received concurrent auditory and visual stimulation during the later stages of incubation. After hatching, chicks were placed in social groups containing 10 to 12 same-age chicks and were individually tested at 24 hr of age in a simultaneous choice test between the familiar bobwhite call (Call B) and the unfamiliar variant of the call (Call A), as in the Experiment 3.

Results and Discussion

As can be seen in Table 3, subjects incubated in isolation and exposed to prenatal visual stimulation at the same time they were exposed to an individual maternal call demonstrated a significant preference for that familiar call at 24 hr following hatching ($p < .01$). Analysis of the latency of response by the Wilcoxon test also revealed a preference for the familiar maternal call: Subjects showed shorter latencies in their response to the familiar bobwhite call (Call B) than to the unfamiliar call (p

$< .01$). This demonstration of individual auditory learning is in sharp contrast to the results of Experiment 3, in which embryos incubated in physical isolation (but not exposed to visual stimulation) did not exhibit a preference for the familiar maternal call and supports the notion that increasing the amount of sensory stimulation available to physically isolated embryos facilitates early auditory learning.

The results from the present experiment likewise differ from the results obtained from communally incubated bobwhite embryos in a previous study (Lickliter & Hellewell, 1992). In that study, communally incubated embryos that received visual stimulation concurrently with exposure to the maternal call failed to learn that maternal call, whereas control embryos that were not exposed to unusually early visual input during exposure to the call did learn the individual maternal call. The findings from the present experiment, which show that exposure to unusually early visual input in the absence of specific sensory stimulation from broodmates leads to successful auditory learning, provides yet more evidence that prenatal learning requires some optimal level of background stimulation to be effective. Taken together, the results of the present experiment and the results of the Lickliter and Hellewell (1992) study indicate that there is some optimal level of overall sensory stimulation bobwhite embryos require during the prenatal period; substantial increases (e.g., exposing communally incubated embryos to concurrent auditory and visual stimulation) or substantial decreases (e.g., incubating embryos in physical isolation from broodmates) in the range of stimulation normally present results in deficits in early perceptual functioning. A similar conclusion was reached by Radell and Gottlieb (1992) in their study of developmental intersensory interference in duckling embryos and hatchlings. As discussed earlier, Radell and Gottlieb (1992) showed that significantly augmented prenatal stimulation of the vestibular, tactile, and proprioceptive systems can also interfere with normal patterns of early auditory learning.

General Discussion

By way of review, the experiments of this study examined the effects of attenuated prenatal sensory stimulation on subsequent auditory and visual responsiveness to maternal cues in bobwhite quail chicks. Results revealed that chicks denied direct physical contact with broodmates during the late stages of incubation exhibit patterns of perceptual functioning different from chicks allowed ongoing vestibular and tactile stimulation from broodmates during late incubation. Specifically, chicks incubated in physical isolation responded to maternal auditory cues into later stages of postnatal development (Experiment 1) and failed to respond to maternal visual cues at ages normally reared chicks display such species-specific visual responsiveness (Experiment 2). In addition, embryos incubated in physical isolation failed to exhibit early auditory learning of an individual maternal call, a behavior reliably seen in communally incubated embryos (Experiment 3). However, isolation-reared embryos receiving visual stimulation concurrently with exposure to an individual maternal call did demonstrate prenatal auditory learning (Experiment 4).

These results indicate that a substantial decrease in the amount of sensory stimulation normally present in the prenatal

environment can result in altered prenatal and postnatal perceptual functioning. Specifically, these results demonstrate a slowing in the rate of species-specific perceptual development when compared with unmanipulated hatchlings. This finding is complemented by results obtained in related studies concerned with the effects of substantial increases in the amount of sensory experience present prenatally (Gottlieb et al., 1989; Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992). These studies all found that increases in the range of stimulation normally present in the prenatal period can also result in deficits in the early perceptual capacities of avian embryos and hatchlings.

In the more general sense, the results of this study are consistent with a view of perceptual development initially proposed by Schneirla (1959, 1965) over 30 years ago. Schneirla argued that quantitative aspects of sensory stimulation play a critical role in shaping the behavioral-perceptual repertoire of an organism during its earliest stages of development. More pertinent to the present findings, he also maintained that the effectiveness of a particular stimulus depends not only on its specific quantitative value but also on the properties of the organism's receptors, the animal's general state of arousal, its experiential history, and its developmental condition (Schneirla, 1965). More recently, a number of investigators have elaborated and extended Schneirla's ideas and have generated a body of empirical evidence in support of his position (i.e., Karmel, Gardner, & Magnano, 1991; Lewkowicz, 1991; Turkewitz, Lewkowicz, & Gardner, 1983).

The unique role that quantitative aspects of stimulation play in early sensory-perceptual functioning is illustrated by the findings of a study by Lewkowicz and Turkewitz (1980). They showed that when human infants are given the opportunity to equate auditory and visual inputs on the basis of their intensity, they do so without any prior training. The spontaneous propensity to equate stimulation across modalities on the basis of intensity differs markedly from adults' behavior in the same experimental task. In contrast to infants, adults do not exhibit spontaneous cross-modal matching of intensity. Similar evidence of intensity-based, nondifferential responding to stimulation from different modalities by infants has been obtained by Spear and his colleagues in work with neonatal rat pups (Spear, Kraemer, Molina, & Smoller, 1988; Spear & Kucharski, 1984; Spear & Molina, 1987). Spear and his colleagues found that following the acquisition of conditioned suppression to a stimulus in a given modality, rat pups (but not adults) can exhibit transfer of conditioned suppression to stimuli from other modalities. Such intersensory equivalence appears to be uniquely characteristic of the neonatal period and is thought to be the result of quantity-based response mechanisms that mediate behavioral functioning during the earliest stages of development (Turkewitz et al., 1983).

In addition to evidence that intensity of stimulation provides a basis for intersensory responsiveness during infancy, there is also a substantial body of evidence showing that a stimulus of a fixed value can have markedly different effects on the neonate depending on the amount of concurrent stimulation provided in the same or different sensory systems or on the neonate's level of arousal. For example, Lewkowicz and Turkewitz (1981) showed that human infants' visual preferences for lights of different brightness could be modified by first prestimulating

them with a pulse of white noise. Infants who were prestimulated with sound reduced their looking at a brighter light and increased looking at the dimmest light compared with a control group of unstimulated infants. Gardner and Karmel (1984) found that neonates who are tested just after they have been fed, and therefore when their arousal level is relatively low, prefer to look most at rapidly flashing visual stimuli and look least at slowly flashing ones. In contrast, the same infants prefer to look most at slowly flashing visual stimuli when they are tested in a highly aroused condition (i.e., just before feeding). Gardner, Lewkowicz, Rose, and Karmel (1986) obtained a similar shift in visual preferences, but in this case the shift in preference was obtained by prestimulating neonates with either auditory or visual stimulation before testing for their preferences.

Taken together, these findings show that it is possible to modify the attentional "value" of a given stimulus or range of stimuli by manipulating the infant's overall level of arousal and that this modification can be achieved by manipulating either the organism's internal state or the nature of external sensory inputs, regardless of modality. This pattern of results has led Karmel et al. (1991) to argue that neonatal behavioral responsiveness is the result of an interaction between arousal and attentional systems and that one system cannot be understood without consideration of the other. In other words, the attentional value of a given stimulus cannot be understood simply by referring to its specific physical attributes. Rather, attentional value can only be understood when it is considered within the overall context of the organism, including the interaction of both internal and external sources of stimulation and the resultant level of organismic arousal.

The overall pattern of results from the present experiments is consistent with this view and suggests that the perceptual development of precocial birds may also be best understood by considering the interaction of attentional and arousal systems. As with human infants, the response of bobwhite quail embryos to a specific sensory input (an individual maternal call) was very different depending on whether concurrent sensory stimulation was present. Furthermore, the fact that prenatal learning of a specific maternal call can be obtained either in the presence of broodmates (Lickliter & Hellewell, 1992) or in the absence of broodmates but in the presence of concurrent visual stimulation (Experiment 4) indicates the nonspecificity of sensory stimulation levels necessary for prenatal auditory learning to occur.

Additional evidence for this view comes from Radell and Gottlieb's (1992) experiments showing that duck embryos fail to learn a specific duck maternal call in the presence of substantially augmented multimodal stimulation. These results suggest that when the sum of stimulation exceeds some optimal range, the embryo no longer attends to the additional external sensory input provided and thus does not incorporate the consequences of specific prenatal stimulation into its subsequent perceptual repertoire. Evidence that demonstrates the converse of this effect comes from Experiments 1 and 2 of this study. The results from these two experiments show that when embryos are deprived of the normally available vestibular, tactile, and proprioceptive stimulation provided prenatally by broodmates, they do not attend to augmented visual stimulation in a way that allows them to demonstrate its consequences when tested postnatally.

It is important to note that recent results from various investigators working with a variety of animal infants (rather than embryos) have likewise shown that sensory overstimulation or deprivation can result in detrimental effects on the development of intersensory integration (Foreman & Altaha, 1991; Kenny & Turkewitz, 1986; McBride & Lickliter, 1994; Symons & Tees, 1990). However, the data from these studies and the present work are not sufficient to allow any a priori predictions regarding the optimal levels or thresholds of stimulation necessary for the achievement of normal or typical perceptual development in embryos or neonates. What remains to be explored in future studies are the specific parameters of arousal-based response mechanisms that would allow the identification of the levels or thresholds of stimulation associated with normal functioning and the underlying neural structures responsible for these mechanisms.

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