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Early Visual Experience Affects Postnatal Auditory Responsiveness in Bobwhite Quail (*Colinus virginianus*)

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Results from 6 experiments suggest perinatal visual experience interferes with postnatal auditory responsiveness in bobwhite quail (*Colinus virginianus*). Light- or dark-reared control chicks responded similarly to bobwhite maternal Calls A or B following hatching. Light-reared chicks that experienced 10 min/hr of Call A or B from hatching until testing preferred the familiar call at Days 2–4, but dark-reared chicks preferred the familiar call at all ages. Increased amounts of exposure to maternal calls during postnatal Days 1–2 led to auditory responsiveness deficits in light-reared chicks. Similarly, embryos exposed to 10 min/hr of prenatal visual cues required 48 hr of postnatal Call A or B exposure to demonstrate auditory discrimination. These findings highlight the linkages between developing auditory and visual systems during infancy.

Almost 20 years ago, Johnston (1985) proposed that young organisms learn within a developmental system comprising both external influences (e.g., stimuli present within an ecological niche) and internal influences (e.g., status of sensory system development, physiological organization, and experiential history of organism). Previous empirical studies using this systems approach have explored the processes by which young birds (Gottlieb, Tomlinson, & Radell, 1989; Lickliter & Hellewell, 1992; Sleigh, Columbus, & Lickliter, 1996) and mammals (DeCasper & Spence, 1986; Lariviere & Spear, 1996; Mateo, 1996; Poeggel & Braun, 1996; Smotherman & Robinson, 1985; Tees, Buhrmann, & Hanley, 1990) learn to recognize and discriminate between sensory stimuli during early development. Collectively, results from these studies provide strong evidence that early discrimination ability becomes canalized through continuous transactions between the organism's environment and its species-typical biological development. Several theorists have suggested that these experiential transactions between internal and external factors allow young organisms to quickly adapt to changing contextual conditions during ontogeny (Germana, 1989; Johnston, 1981, 1985; Lickliter, 1996; Miller, 1997).

One organismic factor affecting how animals process information from their environments is their species-typical pattern of early biological organization and perceptual development (Gottlieb, 1983, 1993; Klein & Mowrer, 1989; Miller, 1997). For example, previous research has shown that the sensory systems of birds and mammals do not become functional at the same time in development, but rather they follow an invariant, sequential pattern of onset of function: tactile, vestibular, chemical, auditory, and visual (Gottlieb, 1971; Mistretta & Bradley, 1978). This sequential onset of the sensory systems has been shown to affect subsequent perceptual responsiveness as well as early learning capacity (Gottlieb et al., 1989; Lickliter & Hellewell, 1992). Importantly, Turkewitz and Kenny (1982) suggested that competition within and between the sensory systems may regulate the development of emerging perceptual capabilities and that modifications of sensory experience to one modality may interfere with the organization of earlier developing sensory systems during development. According to the strong form of this hypothesis, premature stimulation from a later developing sensory modality may cause permanent reorganization of an organism's sensory system, which would change the organism's capacity to process sensory information. A weaker form of this hypothesis proposed by Gottlieb et al. (1989) suggests that early stimulation from a later developing modality may cause transient, but not permanent, changes to the organism's early sensory organization.

In line with these theoretical approaches, several studies have demonstrated that attenuated or augmented perinatal stimulation can affect developing mammalian infants' ability to learn auditory information (DeCasper & Spence, 1986; Poeggel & Braun, 1996; Spear & McKinzie, 1994). For example, Poeggel and Braun (1996) found that infant degus (*Octogon degus*) that receive attenuated experience with species-typical maternal vocalizations during nursing demonstrate functional auditory learning deficits later in

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development. Work with other animal species has demonstrated that premature stimulation from a later developing sensory system (i.e., visual) can interfere with normal functioning in an earlier developing system (i.e., auditory or olfactory), leading to deficits in normal perceptual development (Gottlieb et al., 1989; Kenny & Turkewitz, 1986; Lickliter, 1990a, 1990b). More specifically, the particular types (Sleigh & Lickliter, 1996), amounts (Radell & Gottlieb, 1992; Sleigh & Birchard, 2001; Sleigh & Lickliter, 1995, 1997), and timing (Sleigh & Lickliter, 1998) of sensory stimulation encountered by the young organism shape perceptual functioning and learning capacity during both prenatal and early postnatal periods.

Although studies of avian and mammalian embryos have led to a greater understanding of prenatal learning capacity (see Smotherman & Robinson, 1998, for a review), few studies have examined postnatal perceptual discrimination capacity in avian species during the first few days following hatching. It is important to note that early auditory system development may show different developmental trajectories in response to changing contextual conditions and the altered status of the organism's sensory system hierarchy. In addition, it is still relatively unclear whether any observed changes in early postnatal discrimination capacity are permanent or transient in nature. The present experiments were broadly designed to examine how early postnatal auditory responsiveness to maternal cues is altered by increasing or decreasing the amount of visual experience chicks receive during the periods immediately prior to and following hatching.

General Method

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

Subjects

Subjects were 657 incubator-reared bobwhite quail (*Colinus virginianus*) chicks. Fertile, unincubated eggs were received weekly from a commercial supplier and set in a Petersime Model I incubator (Petersime Inc., Zutte, Belgium), maintained at 37.5 °C and 80%–90% relative humidity. To produce species-typical amounts of vestibular stimulation, an internal incubator motor automatically turned egg trays every 1.5 hr throughout the first 20 days of incubation. 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, we used as subjects only those birds that hatched between the last half of Day 22 and the first half of Day 23 of incubation. The embryo's age is calculated on the basis of the 1st 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 for 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 onset of experimental manipulation or the time of testing were their own embryonic and postnatal vocalizations (and those of their brood mates) 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 8–14 same-aged chicks to mimic naturally occurring brood conditions (Stokes, 1967). In natural settings, bobwhite quail chicks hatch in groups of 8–14 same-aged siblings and leave the nest 1 day after hatching. Young hatchlings continue to interact with conspecifics during early development and rely on adult quail, usually the mother and father, for warmth and foraging locations for 4–5 weeks following hatching (Stokes, 1967). Because their visual range is often restricted, they vocalize frequently to communicate within their social group and are responsive to species-typical auditory cues as hatchlings (Heaton, Miller, & Goodwin, 1978) and adults (Gatehouse & Shelton, 1978). The primary vocalizations to which young quail chicks would normally be exposed consist of contentment and distress calls emanating from conspecifics as well as the maternal incidental, maternal exodus, maternal alarm, and male mating calls emitted by adult quail caregivers (see Heaton et al., 1978, for acoustical details of each call).

Newly hatched chicks are unable to maintain constant body temperature during the first few weeks following hatching (Stokes, 1967). Therefore, 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 to keep chicks warm. Food and water were continuously available throughout the duration of each experiment, except during testing. At the conclusion of each experiment, all chicks were donated to local farmers, landowners, and participants in the State of Virginia Wildlife Habitat Improvement Program.

Testing

Testing was conducted after hatching at 24, 48, 72, or 96 hr (± 3 hr) of age. Each chick was naive at testing and was tested only once in a 5-min simultaneous-choice test. Naive chicks were used to minimize testing effects that would likely occur if subjects were exposed to multiple trials in the arena. Testing occurred in a large circular arena, 160 cm in diameter, surrounded by a wall 24 cm in height and draped by an opaque 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 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 (Sony Corp., Tokyo, Japan) located on a control table. The observer, drawn from trained undergraduates blind to the experimental design, sat at this table and observed each subject's activities through a large mirror positioned above the arena. A system of stopwatches was used to score latency and duration of response, as described below.

During testing, each quail chick was placed singly in the test apparatus equidistant from opposing approach areas. During the 5-min test, subjects were scored on both latency of approach and duration of time spent in each of the two approach areas. In the simultaneous-choice test, the locations of the particular auditory and visual stimuli presented were alternated between chicks to prevent any possible side bias from influencing results. Each chick was tested only once, and latency of response was scored as the amount of time (in seconds) that elapsed from the onset of the trial until the bird entered an approach area. Duration was scored as the cumulative amount of time (in seconds) the 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 s across the 300-s test trial 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 s over the course of the 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 Analyses

The primary data of interest in each experiment were the three specific measures of preference (derived from latency and duration of response) for the auditory and visual stimuli presented during the trial. Differences in the latency of initial response and 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. In addition, we used the chi-square goodness-of-fit test to analyze measures of chicks' individual preference. This nominal measure was assigned to any subject that stayed in one approach area for more than twice as long as they stayed in the other area.

We chose nonparametric tests for several reasons. First, previous studies using methods similar to those reported here have shown that chicks' mean response latencies and durations vary widely within a single experiment and across experiments (e.g., Lickliter & Lewkowicz, 1995; Lickliter & Virkar, 1989). Our data from the present experiments showed similar patterns of variance. The extreme scores often obtained in measuring response latency and duration make measures of central tendency harder to interpret. Nonparametric statistics are appropriate when assumptions about normal variance in the population cannot be made, when extreme scores or outliers are common, when nominal data are obtained, and when ordinal data obtained can be rank ordered (Thorne & Giesen, 2000). These conditions were met in our experiments. Finally, we used a Bonferroni correction (Hays, 1994) in each experiment to minimize Type I error. With this correction, significance levels of $p < .004$ were used in all experiments except for Experiment 5, where significance values were set at $p < .008$. All reported p values are two-tailed.

Experiment 1: Maternally Naive Chicks' Preference for Two Variants of the Bobwhite Maternal Call

Previous studies have demonstrated that bobwhite quail chicks initially direct their social preferences on the basis of available maternal auditory cues. Additionally, chicks show a naive preference for the bobwhite maternal call over a species-atypical chicken maternal call at both 24 and 48 hr following hatching. By 72 hr of age, chicks require combined maternal auditory and maternal visual cues to direct social preference (Lickliter, 1994; Lickliter & Virkar, 1989). Although bobwhite hatchlings initially demonstrate a preference for species-typical over species-atypical maternal auditory information, it remains unclear whether maternally naive chicks prefer one individual call over another. The current experiment examined whether socially reared bobwhite quail chicks would demonstrate a naive preference for either of two individual variants of the bobwhite maternal call (Call A and Call B) at 1–4 days of postnatal age.

Method

Subjects were 84 bobwhite quail (*Colinus virginianus*) chicks, drawn from seven different hatches to control for possible between-batch variation in subjects' behavior. Following hatching, chicks were placed in large plastic tubs (25-cm wide × 15-cm high × 45-cm long) that contained 10–14 same-aged chicks to mimic naturally occurring brood conditions (Stokes, 1967). Chicks were socially reared in 24-hr lighted conditions from hatching until testing and were maternally naive at the time of testing.

Chicks were individually tested at 24, 48, 72, or 96 hr following hatching in a simultaneous-choice test between two individual variants of the bobwhite maternal call (Call A and Call B). These calls were recorded in the field and are similar in phrasing, call duration, repetition rate, and dominant frequency (see Heaton et al., 1978, for acoustical details). The calls were broadcast at a uniform peak intensity of 65 dB (A) during testing, as measured by a Bruel and Kjaer Model 2232 sound-level meter (B&K Instruments, Marlborough, MA) placed 113 cm equidistant from each speaker. The presentation of Call A and Call B was counterbalanced across trials to control for possible side bias in chicks' responses. Food and water were continuously available to subjects throughout the experiment, except during testing.

Results and Discussion

Results are illustrated in Tables 1 and 2. Chicks did not demonstrate a naive preference for Call A or Call B at 24, 48, 72, or 96 hr following hatching. Analysis of latency and duration scores further supported these results, with chicks showing no differences in latency or duration scores at 24, 48, 72, or 96 hr. It is important to note that chicks in this experiment received no prior exposure to either Call A or Call B during prenatal or postnatal rearing, so these results suggest that chicks do not naively prefer maternal Call A or Call B during early development. The next experiment examined whether postnatal exposure to a particular bobwhite maternal call would result in chicks' demonstrating a preference for that familiar call in subsequent auditory testing.

Experiment 2: Patterns of Postnatal Auditory Discrimination in Light-Reared Bobwhite Quail

Previous research has demonstrated that bobwhite quail chicks can discriminate between individual bobwhite maternal calls and learn an individual bobwhite maternal call during the prenatal period. For example, embryos that have been incubated socially and exposed to an individual bobwhite maternal call during the last 24–36 hr of incubation can reliably learn this call and remember it for at least 24 hr following exposure (Honeycutt & Lickliter, 2001; Lickliter & Hellewell, 1992; Lickliter & Lewkowicz, 1995; Sleigh et al., 1996). However, embryos that have not been exposed to either call do not show a naive preference for either maternal call

Table 1
Preference of Light- and Dark-Reared Control Chicks in Simultaneous Auditory Choice Tests in Experiments 1 and 3

			Preference		
Age (in hr)	*n*	*n* responding	Bobwhite maternal Call A	Bobwhite maternal Call B	No preference
Experiment 1: Light-reared control					
24	20	19	4	6	9
48	20	18	2	8	8
72	20	16	4	8	4
96	24	16	4	4	8
Experiment 3: Dark-reared control					
24	20	18	3	9	6
48	20	16	3	8	5
72	22	16	3	9	4
96	26	16	3	8	5

Table 2
Means and Standard Deviations of Latency and Duration Scores of Light- and Dark-Reared Chicks in Simultaneous Auditory Choice Tests in Experiments 1 and 3

		Latency				Duration			
		Bobwhite maternal Call A		Bobwhite maternal Call B		Bobwhite maternal Call A		Bobwhite maternal Call B	
Age (in hr)	*n* responding	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Experiment 1: Light-reared control									
24	19	108.53	99.00	75.32	83.51	46.26	39.37	58.11	49.87
48	18	106.22	111.82	93.56	105.52	26.22	24.74	48.83	37.83
72	16	131.00	127.63	78.38	75.68	49.94	63.84	49.06	32.04
96	20	49.69	76.57	100.50	108.90	43.50	60.97	36.81	45.36
Experiment 3: Dark-reared control									
24	18	137.39	121.75	44.17	35.93	33.72	34.80	57.72	47.14
48	16	132.88	116.49	80.38	60.71	33.00	34.42	51.81	38.87
72	16	140.75	118.75	25.44*	20.34	30.00	41.19	49.81	57.61
96	16	75.94	113.03	71.88	98.44	41.63	58.86	37.44	45.23

* $p < .004$ (Wilcoxon signed-ranks test).

when tested postnatally (Lickliter & Hellewell, 1992). The pattern of auditory perceptual learning that bobwhite quail chicks display in the first several days following hatching remains unexplored. The ability to learn an individual maternal call following hatching would likely be advantageous to the young organism, and several studies have demonstrated such learning ability in other precocial bird species, including pheasants, domestic chickens, gulls, and ducks (Bailey & Ralph, 1975; Fait, 1981; Gottlieb, 1988; Impekoven, 1976; Radell & Gottlieb, 1992). The present experiment examined whether postnatal exposure to an individual bobwhite maternal call would result in auditory learning of that maternal call in bobwhite quail chicks.

Method

Subjects were 159 bobwhite quail (*Colinus virginianus*) chicks, drawn from nine separate hatches to control for possible between-batch variation in subjects' behavior. Following hatching, chicks were placed in large plastic tubs (25 cm wide × 15 cm high × 45 cm long) that contained 10–14 same-aged chicks and were exposed to 10 min/hr of a recorded individual bobwhite maternal call in 24-hr lighted conditions from hatching until testing. To counterbalance for possible differences in ability to learn specific maternal calls, chicks were divided into two groups. Chicks in Group 1 ($n = 77$) were exposed to bobwhite maternal Call A, and chicks in Group 2 ($n = 82$) were exposed to bobwhite maternal Call B.

The calls were broadcast to hatchlings through a Marantz Model PMD 221 cassette tape recorder (Marantz America, Inc., Itasca, IL) located 40 cm from the center of the tub. Calls were presented at a peak intensity of 65 dB (A), as measured by a Bruel and Kjaer Model 2232 sound-level meter (B & K Instruments, Marlborough, MA) placed inside the tub. Testing occurred at 24, 48, 72, or 96 hr following hatching. Chicks were presented with a simultaneous-choice test between the familiar and the unfamiliar variant of the bobwhite maternal call, and their responses and choices were recorded as described in the General Method section.

Results and Discussion

Results are shown in Tables 3 and 4. Chicks receiving 10 min/hr of exposure to an individual variant of the species-specific bobwhite maternal call (Call A or Call B) demonstrated a significant preference for that familiar call over the unfamiliar bobwhite maternal call at 48 hr, $\chi^2(2, N = 38) = 29.26$, $p < .001$; 72 hr, $\chi^2(2, N = 38) = 36.99$, $p < .001$; and 96 hr, $\chi^2(2, N = 39) = 61.38$, $p < .001$, following hatching. Measures of latency and duration of response also supported these patterns of preference, with chicks demonstrating shorter latencies and longer durations of preference for the familiar bobwhite maternal call over the unfamiliar call at 48 hr ($z = 3.88$ for latency, $z = 4.30$ for duration, $p < .001$ in both cases), 72 hr ($z = 4.89$ for latency, $z = 5.18$, for duration, $p < .001$ in both cases), and 96 hr ($z = 5.09$ for latency, $z = 5.44$ for duration, $p < .001$ in both cases).

Table 3
Preference of Chicks Exposed to 10-min/hr Postnatal Call A or B in Simultaneous Auditory Choice Tests in Experiments 2 and 4

			Preference		
Age (in hr)	*n*	*n* responding	Familiar bobwhite maternal call	Unfamiliar bobwhite maternal call	No preference
Experiment 2: Postnatal light reared					
24	37	37	17	9	11
48	40	38	28**	2	8
72	42	38	30**	1	7
96	40	39	36**	0	3
Experiment 4: Postnatal dark reared					
24	41	40	25**	9	6
48	40	39	34**	2	3
72	40	39	32**	3	4
96	40	36	34**	1	1

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

Table 4
Means and Standard Deviations of Latency and Duration Scores of Light- and Dark-Reared Chicks in Simultaneous Auditory Choice Tests in Experiments 2 and 4

		Latency				Duration			
		Familiar bobwhite maternal call		Unfamiliar bobwhite maternal call		Familiar bobwhite maternal call		Unfamiliar bobwhite maternal call	
Age (in hr)	*n* responding	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Experiment 2: Postnatal light reared with 10 min/hr Call A or B									
24	37	47.73	54.33	123.68	124.73	90.38	67.00	51.95	54.08
48	38	70.05**	77.03	192.95	130.56	88.26**	60.23	18.50	30.12
72	38	49.61**	60.50	236.18	111.52	119.97**	78.40	7.63	13.96
96	39	34.64**	33.46	219.92	123.39	105.72**	50.62	7.72	13.48
Experiment 4: Postnatal dark reared with 10 min/hr Call A or B									
24	40	76.88*	76.56	181.73	134.38	102.58*	77.01	38.90	63.26
48	39	53.64**	58.73	251.38	105.70	124.03**	80.10	12.21	34.61
72	39	49.67*	70.01	172.23	140.55	87.23**	60.71	16.97	36.21
96	36	62.00**	54.15	233.94	112.51	101.33**	56.71	6.00	10.82

* $p < .004$ (Wilcoxon signed-ranks test). ** $p < .001$ (Wilcoxon signed-ranks test).

Individual analyses for chicks exposed to each call showed no differences in the ease with which chicks learned Call A or Call B across all ages tested.

Previous studies of prenatal auditory learning in bobwhite quail embryos indicated that embryos that receive exposure to a particular bobwhite maternal call can learn and remember this call following 24 hr of prenatal exposure (i.e., Honeycutt & Lickliter, 2001; Lickliter & Hellewell, 1992; Lickliter & Lewkowicz, 1995). Results from the current experiment stand in contrast to these earlier prenatal studies, in that chicks in this experiment were not able to successfully discriminate between two individual bobwhite maternal calls with less than 48 hr of postnatal exposure. It is important to note that in the earlier studies, bobwhite embryos were exposed to maternal auditory stimulation during the 24–36 hr immediately prior to hatching. During this time, visual experience was dramatically attenuated by the egg shell and innershell membrane.

The present results suggest that some functional distinction may exist between prenatal and postnatal patterns of auditory learning in bobwhite quail embryos and chicks. More specifically, a particular amount of auditory sensory stimulation presented during the prenatal period (i.e., 240 min) apparently provides chicks with enough auditory experience for successful auditory learning. In contrast, the same amount of exposure to the maternal call presented during the postnatal period does not lead to a preference for the familiar call. An obvious difference between prenatal and postnatal periods of development in this species is that following hatching, the quail visual system begins to receive ongoing experience from the posthatch environment. Because chicks in this experiment required up to 48 hr to successfully learn an individual maternal call during the early postnatal period (see Table 3), it is possible that visual experience interfered with chicks' early processing of auditory information, which resulted in altered patterns of postnatal auditory responsiveness. The next two experiments were designed to further examine this possibility. Experiment 3 served as a control for Experiment 4 by examining dark-reared chicks' naive preference for Call A versus Call B.

Experiment 3: Effects of Postnatal Dark Rearing on Chicks' Naive Auditory Preferences for Two Variants of the Bobwhite Maternal Call

Method

The procedures used in this experiment paralleled those used in Experiment 1, with the exception that chicks were dark reared following hatching. Subjects were 88 bobwhite quail (*Colinus virginianus*) chicks, drawn from eight different hatches to control for possible between-batch variation in subjects' behavior. Following hatching, chicks were placed in a darkened portable brooder and reared in groups of 10–14 chicks from hatching until testing at 24, 48, 72, or 96 hr following hatching. The brooder was equipped with a heating element set to maintain an ambient air temperature of approximately 30 °C. The brooder was placed in a darkened room and covered with black paper and black fabric to eliminate the opportunity for ongoing postnatal experience with patterned light. Although we could not be sure that this manipulation eliminated all visual experience for each subject, the dark-rearing condition drastically attenuated normal amounts of postnatal visual stimulation.

Following dark rearing, subjects were tested in a simultaneous-choice test between two individual bobwhite maternal calls (Call A and Call B), as in the previous experiments. Immediately prior to testing, chicks were removed from the darkened brooder and allowed to adjust their eyes to the light of the testing room for a period of 1–2 min, as in previous studies (Columbus & Lickliter, 1998; Lickliter, Lewkowicz, & Columbus, 1996).

Results and Discussion

Results are shown in Tables 1 and 2. Dark-reared chicks did not demonstrate a naive preference for Call A or Call B at 24, 48, 72, and 96 hr following hatching. Analysis of latency and duration scores supported these patterns of preference, with chicks showing no differences in duration at any age tested and no differences in latency at 24, 48, and 96 hr following hatching. Although chicks did demonstrate significantly shorter latency scores in their response to Call B at 72 hr ($z = 3.15$, $p < .004$), these scores were not supported by measures of individual preference or duration scores. These results parallel those observed in Experiment 1 and indicate that hatchlings were not more responsive to either individual variant of the bobwhite maternal call at any age tested following hatching. Thus, the dark-rearing procedure did not appear to affect chicks' naive preferences for unfamiliar bobwhite maternal calls.

Experiment 4: Patterns of Postnatal Auditory Discrimination in Dark-Reared Bobwhite Quail

Results from Experiment 2 suggest that initial visual experience following hatching can potentially interfere with chicks' ability to learn auditory information during the first days following hatching. These findings are suggestive of Turkewitz and Kenny's (1982) sensory system interference hypothesis, which states that stimulation provided from a later developing sensory system (such as visual) to an early developing sensory system (such as auditory) may interfere with development or responsiveness of the earlier developing sensory system. Applying this sensory system limitations hypothesis to the current study suggests that attenuating visual experience following hatching might enable chicks to learn auditory information more readily than chicks provided ongoing visual experience. Recall that chicks in Experiment 2 did not demonstrate a significant preference for the bobwhite maternal call until 48 hr of postnatal exposure. The current experiment examined the possibility that attenuated postnatal visual experience would facilitate postnatal auditory learning, allowing chicks to display similar patterns of perceptual learning as those exhibited by embryos. Bobwhite embryos have natural limitations on visual system input (as a result of their positioning in the egg). This experiment assessed whether chicks denied visual experience following hatching would also learn an individual maternal call after only 24 hr of exposure, paralleling the results obtained from previous studies with bobwhite embryos (Lickliter & Hellewell, 1992).

Method

Subjects were 161 bobwhite quail (*Colinus virginianus*) chicks, drawn from 12 separate hatches to control for possible between-batch variation in subjects' behavior. Following hatching, chicks were divided into two groups. Chicks in Group 1 ($n = 80$) were exposed to 10 min/hr of an individual bobwhite maternal call, Call B, from hatching until testing. Chicks in Group 2 ($n = 81$) were exposed to 10 min/hr of a different bobwhite maternal call, Call A, from hatching until testing. The calls were broadcast through a Marantz Model PMD 221 cassette tape recorder placed on top of a portable brooder at a peak intensity of 65 dB (A), as measured by a Bruel and Kjaer Model 2232 sound level meter placed in the center of the portable brooder 20 cm directly underneath the tape recorders.

All chicks were reared in groups of 10–14 conspecifics in a darkened portable brooder from hatching until testing at 24, 48, 72, or 96 hr, as in the previous experiment. Immediately prior to testing, chicks were removed from the dark-rearing brooder and allowed to adjust their eyes to the light of the testing room for a period of 1–2 min, as in the previous experiment. Food and water were continuously available to subjects throughout the duration of the experiment, except during testing.

Results and Discussion

Results are shown in Tables 3 and 4. Dark-reared chicks exposed to 10 min/hr of an individual bobwhite maternal call demonstrated a significant preference for the familiar call over the unfamiliar call at 24 hr, $\chi^2(2, N = 18) = 15.65$, $p < .001$; 48 hr, $\chi^2(2, N = 16) = 50.92$, $p < .001$; 72 hr, $\chi^2(2, N = 16) = 41.69$, $p < .001$; and 96 hr, $\chi^2(2, N = 16) = 60.5$, $p < .001$, following hatching. Measures of latency and duration of response supported these patterns of preference, with chicks showing significantly shorter latencies and durations of response to the familiar call at 24 hr ($z = 3.17$ for latency, $z = 2.87$ for duration, $p < .004$ in both cases), 48 hr ($z = 4.75$ for latency, $z = 5.37$ for duration, $p < .001$ in both cases), 72 hr ($z = 3.36$ for latency, $p < .004$; $z = 4.17$ for duration, $p < .001$), and 96 hr ($z = 4.92$ for latency, $z = 5.15$ for duration, $p < .001$ in both cases) following hatching.

These results indicate that chicks denied normal amounts of initial postnatal visual experience can learn auditory information more quickly than chicks that are allowed normal postnatal visual experience. These results appear to support Turkewitz and Kenny's (1982) intersensory interference hypothesis, in that introducing limitations on visual system experience during early postnatal development effectively reduced competition between the auditory and visual systems and allowed chicks to learn auditory information more readily. On the basis of these results, it appears that reducing competition between the auditory and visual modalities (which is the species-typical case during prenatal development) facilitates auditory learning very early in postnatal development as well.

Experiment 5: Effects of Increased Amounts of Postnatal Auditory Stimulation on Auditory Discrimination in Bobwhite Quail

In Experiment 4, we decreased the amount of postnatal visual stimulation to mimic the lower levels of cumulative sensory stimulation found during prenatal development. Results suggested that this reduction in competing visual stimulation during the first 24 hr of the postnatal period allowed hatchlings to (a) more efficiently process auditory information and to (b) discriminate between two variants of a bobwhite maternal call. These results support conclusions drawn from previous studies that examined how alterations in the overall amount of stimulation affect intersensory development. Specifically, providing chicks with typical levels or moderate increases in the amount of overall stimulation facilitates intersensory perceptual responsiveness, depending on the type of stimulation encountered (Lickliter & Lewkowicz, 1995; Sleigh & Lickliter, 1996, 1997). However, substantial increases in the amount of stimulation impair normal development and lead to increased mortality in quail (Carlsen & Lickliter, 1999; Sleigh & Lickliter, 1995, 1997).

In Experiments 2 and 4, chicks were provided with 10 min/hr exposure to bobwhite maternal vocalizations from hatching until testing. However, an obvious confound arises from the fact that chicks tested at 48 hr have received 240 min of additional auditory stimulation (total = 480 min) when compared with the 24-hr group (total = 240 min). It is possible that the additional amount of auditory exposure received by the 48-hr group affected chicks' ability to discriminate between the two variants of the maternal call and that the 24-hr group had simply not received enough exposure to the call by the time they were tested. The current experiment was designed to unpack the relationship between developmental age and amount of stimulation provided prior to testing. We increased the overall amount of auditory exposure during the first 24 hr following hatching to 20 min/hr (total = 480 min) to match the amount of stimulation that chicks in Experiments 2 and 4 received by 48 hr following hatching.

Method

Subjects were 81 bobwhite quail (*Colinus virginianus*) chicks, drawn from five separate hatches to control for possible between-batch variation in subjects' behavior. Following hatching, chicks were socially light reared and divided into two experiential groups to counterbalance for the type of call to which chicks were exposed. Chicks in Group 1 ($n = 41$) were exposed to 20 min/hr of an individual bobwhite maternal call, Call B, during the first 24 hr following hatching (total stimulation = 480 min). Chicks in Group 2 ($n = 40$) were exposed to 20 min/hr of a different bobwhite maternal call, Call A, during the first 24 hr following hatching (total stimulation = 480 min). The calls were broadcast to chicks as in previous experiments at an intensity of 65 dB (A). Testing occurred at 24 or 48 hr following hatching in a simultaneous auditory choice test between the two variants of the bobwhite maternal call, as in previous experiments. Food and water were continuously available to chicks, except during testing.

Results and Discussion

Results are shown in Tables 5 and 6. Chicks exposed to 20 min/hr of an individual bobwhite maternal call demonstrated no significant preference for either call at 24 hr, $\chi^2(2, N = 39) = 5.99$, $p > .008$, or 48 hr, $\chi^2(2, N = 34) = 2.18$, $p > .008$, following hatching. Measures of latency and duration of response supported these findings, with chicks demonstrating no significant differences in their patterns of response to these two types of maternal auditory stimulation at 24 hr ($z = 0.63$, $p > .008$) or 48 hr ($z = 0.96$, $p > .008$). These results demonstrate that chicks given augmented amounts of auditory information during the first 24 hr following hatching do not prefer either call by 48 hr.

It is important to note that chicks in this experiment received increased amounts of auditory stimulation in conjunction with visual stimulation during the first 24 hr following hatching. In line with previous studies of developmental intersensory interference, it appears that the overall amount of stimulation provided during this period may have exceeded the organisms' capacity to process that information. In other words, instead of improving chicks' ability to learn a maternal call, providing augmented auditory exposure in this experiment appears to have interfered with chicks' auditory discrimination abilities.

In Experiment 2, light-reared chicks that experienced 10 min/hr exposure from hatching until testing at 48 hr (total = 480 min) were able to discriminate between familiar and nonfamiliar maternal calls. In contrast, light-reared chicks in this experiment received the same amount of auditory exposure from hatching until testing but that experience was compressed into the first 24 hr following hatching. Chicks in this condition were unable to discriminate between the maternal call variants, suggesting that simply providing more stimulation is not sufficient to promote auditory processing and preference. In fact, the increased amount of auditory exposure during this period may have been even more detrimental to chicks, in that the overall amount of stimulation exceeded the optimal range of stimulation necessary to facilitate auditory learning. This conclusion is supported by the fact that chicks tested at 48 hr failed to discriminate between the familiar and nonfamiliar calls, even though they had received the same amount of exposure as 48-hr chicks in Experiment 2. These findings rule out the confound of relative differences in amount of stimulation between 24-hr and 48-hr groups in Experiments 2 and 4. In addition, they provide additional support for theories of developmental intersensory interference that focus on how the overall amount of stimulation available to young organisms affects their perceptual organization.

Table 5
Preference of Chicks Exposed to 20-min/hr Call A or B During First 24 hr Following Hatching in Experiment 5

			Preference		
Age (in hr)	*n*	*n* responding	Familiar bobwhite maternal call	Unfamiliar bobwhite maternal call	No preference
24	40	39	18	15	6
48	41	34	15	11	8

Experiment 6: Effects of Prenatal Visual Stimulation on Postnatal Auditory Discrimination

Results from Experiments 2 and 4 support the hypothesis that postnatal visual experience can initially interfere with postnatal auditory discrimination. Results from Experiment 5 suggest that simply increasing the overall amount of auditory experience is not sufficient to promote auditory discrimination when presented in conjunction with visual stimulation. What remains unclear is whether early competition between auditory and visual experience is responsible for developmental intersensory interference. If visual experience does, in fact, interfere with chicks' postnatal auditory processing, then providing embryos with visual experience during prenatal development could potentially delay or alter subsequent postnatal auditory learning. On the basis of this logic, the current experiment was conducted to assess the effects of prenatal visual experience on postnatal auditory learning capacity. We hypothesized that exposing embryos to visual stimulation would accelerate visual system development (see Lickliter, 1990a, 1990b). Furthermore, we hypothesized that this early visual experience would interfere with postnatal auditory learning, even when visual experience was attenuated during postnatal development.

Method

Subjects were 84 bobwhite quail (*Colinus virginianus*) embryos and hatchlings, drawn from 10 separate hatches to control for possible between-batch variation in subjects' behavior. On Day 21 of incubation, subjects underwent an egg-opening procedure to ensure that embryos were able to

Table 6
Means and Standard Deviations of Latency and Duration Scores of Chicks in Simultaneous Auditory Choice Tests in Experiment 5

Age (in hr)	*n* responding	Latency				Duration			
		Familiar bobwhite maternal call		Unfamiliar bobwhite maternal call		Familiar bobwhite maternal call		Unfamiliar bobwhite maternal call	
		M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
24	39	133.49	118.42	162.15	127.48	52.62	60.54	45.00	55.05
48	34	118.88	122.02	140.26	119.25	40.15	45.33	26.85	27.59

see the presented visual stimulation. During this procedure, the shell and innershell membrane over the air space of each subject's egg was removed. The embryo's bill usually penetrates the air space early on Day 21, and at this time the embryo begins to respire and vocalize (Freeman & Vince, 1974). Previous studies have shown that this procedure does not interfere with incubation, postural orientation, species-typical perceptual behavior, or survivability (Banker & Lickliter, 1993; Heaton & Galleher, 1981). Following the egg-opening procedure, opened eggs were placed in a Hovi-bator portable incubator (GQF Manufacturing, Savannah, GA) for the last 24 hr of incubation. This incubator was equipped with a Plexiglas top, which allowed for visual stimulation of the embryos contained within. Temperature and humidity were maintained as in prior incubation, and as a result, embryos in this experiment did not differ in developmental age at hatching from embryos in Experiments 1–5.

To provide prenatal visual stimulation, we incubated subjects in groups of 10–14 same-aged embryos and exposed them 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) for the 24 hr immediately prior to hatching. Thus, chicks received a total of 240 min 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 (total stimulation = 240 min), at which point they were transferred to the darkened portable brooder, as described in the previous experiment. In addition to being dark reared, chicks received postnatal exposure to 10 min/hr of bobwhite maternal Call A ($n = 39$) or Call B ($n = 45$) broadcast from tape players located on top of the brooders, as in previous experiments. Food and water were continuously available to the chicks throughout the experiment, except during testing. Subjects were tested at 24, 48, 72, or 96 hr following hatching using the simultaneous-choice test between Call A and Call B, as in the previous experiments. Immediately prior to testing, chicks were allowed to adjust to the light of the testing room for 1–2 min.

Results and Discussion

Results are shown in Tables 7 and 8. Chicks reared in prenatal light-enhanced and postnatal dark-reared conditions failed to successfully learn the call following 24 hr of exposure, $\chi^2(2, N = 19) = 5.47$, $p > .05$. In contrast, chicks learned the call with 48 hr, $\chi^2(2, N = 20) = 12.10$, $p < .01$; 72 hr, $\chi^2(2, N = 20) = 29.20$, $p < .001$; and 96 hr of exposure, $\chi^2(2, N = 20) = 24.70$, $p < .001$. 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 ($z = 0.20$ 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). Although 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 ($z = 2.30$ for duration, $p < .05$). Chicks did not demonstrate any significant differences in their responsiveness to either maternal call at any age tested.

These results parallel those found in Experiment 2, in which chicks reared in normal, lighted postnatal conditions required 48 hr of postnatal auditory experience to discriminate and prefer a familiar bobwhite maternal call. These findings support the hypothesis that visual experience during late prenatal development can interfere with chicks' ability to learn auditory information during postnatal development. Chicks in the current experiment received 24 hr of visual experience prenatally, during a time they would not normally experience this type of stimulation. This prenatal visual experience was sufficient to delay postnatal auditory learning by 24 hr, even when chicks were dark reared during early postnatal development. In contrast, chicks that did not receive prenatal visual experience and were dark reared during postnatal development learned to discriminate between familiar and nonfamiliar maternal auditory cues by 24 hr following hatching (Experiment 4).

Table 7
Preference of Chicks in Simultaneous Auditory Choice Tests in Experiment 6

Age (in hr)	*n*	*n* responding	Preference		
			Familiar bobwhite maternal call	Unfamiliar bobwhite maternal call	No preference
24	20	19	11	5	3
48	20	20	14*	3	3
72	21	20	18**	0	2
96	23	20	17**	0	3

* $p < .004$ (chi-square test). ** $p < .001$ (chi-square test).

Table 8
Means and Standard Deviations of Latency and Duration Scores of Chicks in Simultaneous Auditory Choice Tests in Experiment 6

		Latency				Duration			
		Familiar bobwhite maternal call		Unfamiliar bobwhite maternal call		Familiar bobwhite maternal call		Unfamiliar bobwhite maternal call	
Age (in hr)	*n* responding	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
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

** $p < .001$ (Wilcoxon signed-ranks test).

General Discussion

The current study examined whether the amount of visual experience provided during late prenatal and early postnatal development affects bobwhite embryos' and hatchlings' ability to learn and remember maternal auditory vocalizations. Results indicated that attenuated amounts of visual stimulation during the early postnatal period can facilitate postnatal auditory discrimination in bobwhite quail chicks. Chicks that were denied typical amounts of postnatal visual stimulation learned maternal auditory information with less exposure than chicks reared in lighted conditions. On the basis of these results, it appears that reducing the overall amount of one type of sensory input (visual) during the period following hatching can facilitate learning of information presented to a different sensory modality (auditory).

These results are consistent with an earlier study (Lickliter & Hellewell, 1992) in this series in which postnatal auditory learning was also facilitated by reductions in the overall amount of postnatal sensory stimulation. Lickliter and Hellewell (1992) reared bobwhite hatchlings in lighted conditions and exposed them to 10 min/hr of postnatal auditory exposure to an individual bobwhite maternal call (Call B) during the first 24 hr following hatching. Hatchlings in this condition showed no preference for the familiar call at 48 hr following hatching. However, hatchlings who were exposed to 10 min/hr of bobwhite maternal Call B in tactile isolation from brood mates (thereby reducing the overall amount of postnatal sensory stimulation) demonstrated a significant preference for the familiar call at 48 hr following hatching. These results suggested that reducing the amount of one type of postnatal sensory stimulation (e.g., tactile contact with siblings) can facilitate postnatal auditory learning. Taken together with the present findings concerning visual stimulation, it appears that reductions in the overall amount of postnatal sensory stimulation can facilitate bobwhite quail chicks' ability to learn maternal auditory information during the initial days following hatching.

The results from Experiments 2 and 4 raise several interesting issues. First, it appears that chicks' auditory learning process is different during prenatal and postnatal development and that these differences may stem from the onset of visual experience following hatching. Previous studies with bobwhite quail have shown that embryos exposed to 10 min/hr of an individual bobwhite maternal call during the 24 hr prior to hatching successfully learn and remember this call for 24 hr following hatching (Honeycutt & Lickliter, 2001; Lickliter & Hellewell, 1992; Lickliter & Lewkowicz, 1995; Sleigh, et al., 1996), but chicks that receive 10 min/hr exposure to the maternal call for the 24 hr following hatching appear unable to learn the maternal call (Experiment 2; Lickliter & Hellewell, 1992). Although light-reared chicks require up to 48 hr to learn an individual bobwhite maternal call (Experiment 2), dark-reared chicks learn the familiar call within 24 hr of exposure following hatching (Experiment 4). From these results, it appears that chicks' ability to learn auditory information in darkened postnatal rearing conditions parallels the pattern of prenatal auditory learning previously reported with bobwhite quail embryos (Lickliter & Hellewell, 1992).

Second, results from Experiment 6 provide partial support for 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 perceptual organization and development. Chicks receiving prenatal visual experience and then denied postnatal visual experience required longer exposure periods to demonstrate postnatal auditory learning than did chicks denied only postnatal visual experience. These results provide greater support for the weak form of developmental intersensory interference proposed by Gottlieb et al. (1989), 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, holds that 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 et al. (1989) and Radell and Gottlieb (1992) suggests that premature stimulation from a later developing sensory modality can cause transient interference effects, likely by overtaxing the organism's developing, but immature, attentional abilities. In the current project, chicks that received premature visual stimulation and were subsequently reared in postnatal darkened conditions required an additional 24 hr of exposure to prefer 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 6).

These findings suggest that postnatal auditory learning may occur more easily when competing sensory stimulation from the visual modality is decreased during the early postnatal period. In other words, reducing competition between emerging sensory modalities during early development can result in enhanced perceptual learning abilities. It is interesting to note that Gottlieb (1993) demonstrated that tactile contact between broodmates is critical for extending early learning capacity in young mallard ducklings. In that study, ducklings reared with normal amounts of tactile stimulation subsequently preferred species-atypical maternal calls over species-typical calls, suggesting that developmental malleability in one modality (i.e., auditory responsiveness) is fostered, rather than impaired, by stimulation from a different modality (i.e., tactile cues). We should note, however, that traditional theories of intersensory interference suggest that impairment in sensory functioning is more likely to occur when stimulation from a later developing modality is presented prematurely in early development, a hypothesis supported by the data presented here. In the present study, premature stimulation from a later developing sensory system (visual) interfered with processing in an earlier developing system (auditory) during the 24-hr period immediately following hatching. In contrast, the tactile system becomes functional prior to the auditory and visual systems, which may explain why Gottlieb (1993) failed to find sensory system interference in chicks reared with tactile stimulation. This interpretation may also explain why some studies have found that augmented tactile stimulation in premature infants facilitates, rather than impairs, physiological development (Field, 1980).

Comparative studies of early intersensory interference have recently gained attention because of their implications for perceptual development in premature human infants (see Lickliter, 2000, for a review). Experimental studies using avian and mammalian fetuses suggest that early sensory functioning is affected by internal characteristics unique to the organism, such as variations in arousal level and neurological organization (Gardner & Karmel, 1995; Gray, 1990; Withington-Wray, Binns, & Keating, 1990) as well as by characteristics of sensory stimulation encountered during early development. It is important for the human literature that findings presented here support the weak form intersensory interference originally proposed by Gottlieb et al. (1989), suggesting that competition between sensory modalities may be reversible in some animal populations. The findings also suggest that auditory learning and discrimination capacity may be enhanced in young organisms by reducing the overall amount of competing stimuli from the visual system, an issue that has recently gained attention from practitioners and researchers studying premature human infants (Als, 1995; Mueller, 1996). Results from Experiment 5 suggest that augmented amounts of postnatal auditory stimulation, in conjunction with normal amounts of postnatal visual stimulation, may disrupt the organism's normal arousal level and thus delay or interfere with the organism's ability to process auditory information. More generally, results from the present study support the growing body of evidence that the sensory systems are strongly linked during the perinatal period and that the type, amount, and timing of stimulation to one sensory modality can influence infants' processing of information from other sensory modalities.

The current study focused on how the type, amount, and timing of perinatal visual stimulation affected auditory learning and discrimination abilities. Although previous studies of intersensory interference have reliably demonstrated that developing sensory systems are sensitive to changes in the overall amount and type of stimulation, it is possible that other systems are affected by variations in the optimal range of stimulation. Future studies should examine the effects of altered sensory experiences on vocalization frequency, orienting behavior, adult–offspring interaction, motor activity, or social responsiveness to conspecifics in developing organisms. These additional measures may assist in unpacking the dynamic and multidimensional nature of perinatal sensitivity to altered sensory stimulation in both animal and human populations.

In summary, results from the present study also provide additional experimental evidence that early learned preferences emerge from ongoing interactions between organisms and their species-typical environments during early development. From this view, the minimal unit for the developmental analysis of species-typical behavior is the developmental system, which comprises both the developing organism and its specific environment or context. Several theorists have suggested that any understanding of early perception, learning, and related 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, 1997; Johnston, 1985; Johnston & Pietrewicz, 1985; King & West, 1987; Kuo, 1967; Lickliter, 1996; Miller, 1985, 1997; West & King, 1987). The present results support this psychobiological systems approach to understanding early perceptual learning processes. Specifically, characteristics of the developing organism, such as interactions between sequentially developing sensory systems, were found to coact with characteristics of the organism's developmental niche, such as the type, amount, and timing of sensory stimulation available, to influence early auditory responsiveness in this species.

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