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Biased Embryos: Prenatal Experience Alters the Postnatal Malleability of Auditory Preferences in Bobwhite Quail

ABSTRACT: Many precocial birds show a robust preference for the maternal call of their own species before and after hatching. This differential responsiveness to species-specific auditory stimuli by embryos and neonates has been the subject of study for more than four decades, but much remains unknown about the dynamics of this ability. Gottlieb [Gottlieb [1971]. *Development of species identification in birds: An enquiry into the prenatal determinants of perception*. Chicago/London: University of Chicago Press] demonstrated that prenatal exposure to embryonic vocalizations serves to canalize the formation of species-specific preferences in ducklings. Apart from this, little is known about the features of the developmental system that serve to canalize such species-typical preferences, on the one hand, and generate novel behavioral phenotypes, on the other. In the current study, we show that briefly exposing bobwhite quail embryos to a heterospecific Japanese quail (JQ) maternal call significantly enhanced their acquisition of a preference for that call when chicks were provided with subsequent postnatal exposure to the same call. This was true whether postnatal exposure involved playback of the maternal call contingent upon chick contact vocalizations or yoked, non-contingent exposure to the call. Chicks that received both passive prenatal and contingent postnatal exposure to the JQ maternal call redirected their species-typical auditory preference, showing a significant preference for JQ call over the call of their own species. In contrast, chicks receiving only prenatal or only postnatal exposure to the JQ call did not show this redirection of their auditory preference. Our results indicate that prenatal sensory stimulation can significantly bias postnatal responsiveness to social stimuli, thereby altering the course of early learning and memory. © 2010 Wiley Periodicals, Inc. Dev Psychobiol

Keywords: prenatal experience; filial preferences; behavioral plasticity; species-typical development; Northern bobwhite

INTRODUCTION

The origin of neonatal attentional biases and perceptual preferences has long been a topic of interest and controversy within developmental science (Moore,

2009). For example, how young animals come to respond selectively to members of their own species (e.g., Gottlieb, 1971; Göth & Hauber, 2004) has been argued to be innate by some investigators (see Graham & Middleton, 1989; Lorenz, 1937; Tinbergen, 1951), the result of a combination of or interaction between innate and non-innate factors (e.g., Marler, 1990), or the result of often non-obvious or non-specific experience during prenatal or early postnatal development (e.g., Bolhuis, 1999; Gottlieb, 1997). A deeper appreciation of the ecology of early development has emerged over the last several decades, providing a wealth of evidence supportive of the latter view. This evidence highlights both the

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importance of normally occurring prenatal experience for the emergence of species-typical behavior (see Casey & Lickliter, 1998; Gottlieb, 1997; Lickliter, 2005; Rogers, 1986; Smotherman & Robinson, 1990, 1995) as well as the often unappreciated *transnatal continuity* between prenatal and postnatal environments, particularly in regards to chemical (i.e., gustatory and olfactory; Coureaud, Schaal, Hudson, Orgeur, & Coudert, 2002; Guiraudie-Capraz et al., 2005; Honeycutt & Alberts, 2005; Wells & Hepper, 2006) and acoustic (Fifer & Moon, 1994; Gottlieb, 1971) stimuli.

A large number of studies employing avian models have shown that prenatal exposure to vestibular, olfactory, auditory, visual and multimodal, audiovisual stimulation can significantly influence the responsivity of precocial birds to stimuli encountered postnatally (e.g., Bertin et al., 2010; Gottlieb, 1991; Green & Adkins, 1975; Honeycutt & Lickliter, 2002; Lickliter, Bahrick, & Honeycutt, 2002; Lickliter & Lewkowicz, 1995). Studies employing prenatal exposure to auditory stimuli, in particular, have demonstrated that, depending upon the timing, quantity and type of stimulus employed, embryos of precocial avian species will readily learn about social stimuli encountered prenatally, as is evidenced by robust preferential approach postnatally (e.g., Gottlieb, 1971; Honeycutt & Lickliter, 2002; Lickliter et al., 2002).

Within their species-typical developmental niche, however, embryos are not only exposed to maternal/parental signals prenatally, as such stimulation provides a natural prelude to postnatal contact and interaction with incubating adult(s). An important question is thus how, apart from merely engendering approach preferences, prenatal auditory stimulation affects both postnatal responsivity to parental signals and species recognition abilities, more generally. The extremely open species-recognition system of precocial birds would intuitively seem to leave them highly vulnerable to “misimprinting” on heterospecific signals. Although this would not be an issue in the vast majority of cases, as most precocial birds rear their own young, many precocial bird species practice intraspecific and/or occasional interspecific brood parasitism (e.g., Åhlund & Andersson, 2001; Krakauer, 2003; Krakauer & Kimball, 2009). Despite the interesting developmental and evolutionary questions suggested by such facts, few studies have sought to investigate the conditions and/or features of the developmental system that might foster more malleable species-typical social preferences, on the one hand, and constrain or buffer embryos and neonates from acquiring species-atypical preferences, on the other.

In one of the few exceptions, Gottlieb (1971, 1997) demonstrated that normally occurring prenatal auditory experience—the vocalizations of the embryo itself, along with those of nearby broodmates—has a canalizing

influence on the development of auditory preferences in mallard ducklings (*Anas platyrhynchos*), biasing embryos such that they reliably prefer the maternal call of their own species over the maternal calls of other species following hatching. Gottlieb argued that such auditory biases likely have a significant influence on later postnatal responsivity to conspecifics, including the more widely studied phenomenon of imprinting to the visual features of conspecifics. In a more recent series of studies, we have explored the effects of social contingencies on the acquisition of preferences for both conspecific and heterospecific auditory stimuli (Harshaw & Lickliter, 2007; Harshaw, Tourgeman, & Lickliter, 2008).

Most precocial birds are highly gregarious and thus frequently encounter conspecific sensory stimulation in a contingent or interactive manner, in many cases beginning even prior to hatching (e.g., Tuculescu & Griswold, 1983). Studies examining the acquisition of filial auditory preferences in precocial birds have nonetheless employed almost exclusively “passive” exposure paradigms, in which chicks and/or embryos are exposed passively to large quantities of auditory stimulation prior to postnatal testing. Northern bobwhite (*Colinus virginianus*) quail, for example, are a highly gregarious, ground-dwelling species that maintain near constant vocal contact (via contact calls) with conspecifics and their mothers during the early postnatal period (Stokes, 1967). A number of studies had found that bobwhite embryos and chicks require at least 240 min of passive exposure to a bobwhite maternal call to acquire a significant preference for that call over a novel bobwhite maternal call (e.g., Foushée & Lickliter, 2002; Lickliter & Hellewell, 1992). We found, however, that making the playback of maternal auditory stimuli contingent upon chick contact vocalizations significantly enhanced the acquisition of preferences for those stimuli in bobwhite chicks (Harshaw & Lickliter, 2007; Harshaw et al., 2008). Day-old chicks provided with a single 5 min session in which they received exposure to an individual variant of a bobwhite (BW) maternal assembly call contingent upon their own vocalizations significantly preferred that variant over a novel BW maternal call (Harshaw & Lickliter, 2007). Chicks provided with a single 5 min contingent exposure to a heterospecific Japanese quail (JQ; *Coturnix japonica*) maternal call, on the other hand, showed a disruption of their species-typical preferences, no longer preferring the BW over the JQ maternal call. Chicks provided with exposure to the JQ call on a variable ratio (VR2) schedule moreover showed a reversal of their species-typical preference, significantly preferring the heterospecific JQ maternal call over the BW maternal call (Harshaw et al., 2008).

In the present study, we sought to expand on these earlier studies, integrating our findings stemming from a

consideration of the interactive nature of the early social ecology of precocial birds with the many studies showing effects of prenatal exposure to social stimuli on the postnatal approach preferences of young birds. We were interested in the impact of prenatal experience with a heterospecific maternal call on the postnatal responsivity of bobwhite chicks to that same stimulus. In particular, we investigated whether a relatively small amount of prenatal exposure to a heterospecific, JQ maternal call during the late stages of incubation would significantly impact the acquisition of a preference following brief postnatal exposure to the call. We were also interested in whether potential synergistic effects of combined prenatal and postnatal exposure to the heterospecific call would depend upon the type of postnatal exposure chicks received (i.e., playback contingent on chick contact vocalizations or yoked, noncontingent exposure).

GENERAL METHOD

Subjects

Fertile, unincubated bobwhite eggs were received weekly from a commercial supplier (Strickland, Pooler, GA) and incubated in a Grumbach BSS 160 Incubator (Munich, Germany), maintained at 37°C and 70% relative humidity. Twenty-four hours prior to hatch, embryos were transferred to a Hova-Bator Model 1590 incubator (G.Q.F. Manufacturing, Savannah, GA), maintained at 37.5°C and 80% relative humidity. After hatching, chicks were transferred to a sound-proof rearing room and placed in groups of 10–15 same-aged chicks, mimicking typical brood conditions for bobwhites in the wild (Stokes, 1967). These groups were housed in plastic tubs (25 cm wide × 15 cm high × 45 cm long) on shelves in a Nuair Model NU-605-500 Animal Isolator (Plymouth, MN). Ambient air temperature was maintained at approximately 35°C in the rearing room (approximately –.5°C per day post-hatch) and 30–32°C in the training/testing room. Chicks thus experienced minimal thermal stress when outside of the rearing room. Except during behavioral training and testing, food and water were available ad libitum. Chicks for each condition were drawn from two or more weekly batches to minimize the influence of any inter-batch variability.

Auditory Stimuli

The auditory stimuli used in the study were a Japanese quail (*Coturnix japonica*) maternal call (Long, Kennedy, & Balaban, 2001; Park & Balaban, 1991) and a Northern bobwhite maternal call (Call B; Heaton, Miller, & Goodwin, 1978), both cleaned of background noise by The Borror Laboratory of Bioacoustics (Columbus, OH). The two calls are functionally similar, both being maternal assembly calls for their respective species, but differ in several acoustic characteristics. The bobwhite maternal assembly call consists of five notes, lasting 3 s in total, and has dominant frequencies of 1.2–1.5 and 2–2.4 kHz. The Japanese quail maternal call also consists of five notes, but is 1.8 s long,

and has dominant frequencies of .75–.85 and 1.6–1.7 kHz. The Japanese and Northern bobwhite quail are distantly related species that do not overlap in their geographical ranges (the bobwhite is a North American species, whereas the Japanese quail is a domesticated form of a species native to Asia). Previous studies have demonstrated that maternally naive bobwhite quail chicks prefer the bobwhite maternal call over the maternal calls of other precocial avian species (Harshaw et al., 2008; Heaton et al., 1978; Lickliter & Virkar, 1989).

Prenatal Auditory Exposures

Prenatal auditory stimulation was delivered via a speaker placed on top of an air vent in the lid of the portable incubator. Sound pressure level was calibrated to a maximum of 65 dB at a point directly beneath this vent using a Brüel & Kjaer Model 2232 sound-level meter (B & K Instruments, Marlborough, MA), prior to eggs being placed in the incubator, clustered at this location. Hatch times were estimated prospectively based on a combination of egg “pipping,” which generally occurs 24–36 hr prior to hatch, and recent hatch statistics. Stimulus deliveries were accomplished via custom software, set to play the Japanese quail maternal call on a loop for 5 min/hr over the course of the last 12 hr of incubation.

Postnatal Training/Testing Apparatus

All training and testing sessions were conducted in a large circular arena (diameter = 130 cm, height = 24 cm) within a sound-attenuated room, non-adjacent to the rearing room. The surface of the arena was constructed of plywood, painted flat black. The sides of the arena were constructed out of sheet metal formed into a circle, covered by a layer of sound-attenuating foam and opaque black cloth. Loudspeakers were hidden on opposite sides of the arena. These were wired to independent RCA SA-155 amplifiers (Fort Worth, TX), each connected both to a Sony CDP-XE370 CD player (Tokyo, Japan), used during testing sessions, and an isolated RCA output channel of an M-Audio Audiophile 2496 Sound Card (M-Audio USA, Irwindale, CA), used during training sessions. A video camera, mounted above the arena, and a microphone, placed beneath the arena, provided continuous visual and auditory monitoring of training and testing sessions. Prior to all sessions, sound pressure levels at the start location for chicks placed in the arena (a point equidistant from both speakers on the periphery of the arena) was calibrated to a maximum of 65 dB for both speakers using a Brüel & Kjaer Model 2232 sound-level meter. At the start of all training and testing sessions, a single chick was placed in an opaque plastic start box at the start location and left for a period of 30–60 s of adjustment prior to the onset of stimulation and/or data collection. All stimulus deliveries and behavioral observations were made using Visual Basic/Excel programs.

Training Sessions

All training sessions were conducted approximately 24 hr following hatching and involved individual exposures to the heterospecific Japanese quail maternal call. During training

sessions, presentation of the call was made contingent upon the occurrence of chick contact vocalizations (i.e., a single playback of the maternal call per chick contact call). Bobwhite chick contact calls are easily distinguishable from other chick vocalizations, each consisting of a string of rapid “peeps” (Stoumbos, 1990). Experimenters were instructed to play the call up to five times non-contingently over the course of the first 60–100 s of training to coax non-vocal chicks to begin vocalizing (see Harshaw & Lickliter, 2007). Any chick that failed to respond to this procedure was removed from the study. The side of call playback in the arena was alternated and balanced across sides during each session to prevent the development of any side-biases in chicks. The timing and location of each playback was recorded automatically in an Excel sheet. These were later imported into another Excel/Visual Basic program designed to read these as scripts and playback calls accordingly. Yoked, noncontingent (YNO) training sessions were thus identical to contingent training sessions except for the absence of systematic contingency between the chick’s vocal behavior and the presentation of the maternal auditory stimulus. As in traditional yoked designs, each chick trained under YNO conditions was yoked individually to another chick that received contingent playback of the maternal call during training. Ours was thus a fully yoked design, without the potential confound of social learning in yoked subjects present in earlier studies of stimulus contingency and filial imprinting (e.g., Bolhuis & Johnson, 1988; ten Cate, 1986; see Harshaw & Lickliter, 2007).

Testing Sessions

All testing sessions took place on Day 2 post-hatch, approximately 24 hr following training for all subjects except the naïve controls, who received no training. Testing sessions were identical across conditions and experiments and consisted of a 5 min simultaneous choice test between the heterospecific Japanese quail and conspecific bobwhite quail maternal calls. Both calls were played at the same repetition rates, from opposite sides of the arena for the duration of the test. The side of call playback was also counterbalanced within each condition. A semicircular approach area, representing approximately 5% of the surface area of the arena, was demarcated around each speaker on the monitor used by experimenters for observing sessions. Upon entry into one of these approach areas the experimenter, blind to the chick’s experimental condition, clicked on one of two buttons on a Visual Basic program. The button was held down until the chick exited the approach area. This provided tallies of entries into both areas, cumulative scores for duration of time spent within each approach area, and scores for latency of approach to each test stimuli.

Data Analyses

Raw duration scores were converted into categorical “preferences” so that Chi-square tests could be performed on their distributions. Chicks failing to spend at least 30 s (10% of the trial) in an approach area were scored as non-responders and excluded from further analyses. Of the remaining subjects, chicks failing to spend at least twice as long in one approach area

as in the other were scored as displaying no preference. A chick was thus scored as displaying a preference for a call only if the chick spent at least 30 s in the approach area for that call and at least twice as long in that approach area as in the other. A latency score of 300 s and a duration score of zero were assigned for any area not entered by a chick during a testing session. Non-parametric tests were employed because the data for most of our conditions did not meet the assumption of normality. Chi-square tests were supplemented with Wilcoxon matched-pairs signed-ranks tests on raw latency and duration scores. In addition, duration and latency scores were converted into proportion of total duration (PTD) and proportion of trial elapsed prior to approach (PTTA) scores, respectively. Between-group comparisons were performed on PTD scores and on PTTA difference scores ($PTTA_{JQ} - PTTA_{BW}$) using Mann–Whitney U (MWU) tests. Effect sizes reported are Glass rank biserial correlational coefficients (r_g) for MWU tests and matched-pairs rank biserial correlational coefficients (r_C) for Wilcoxon tests. All statistical tests were performed using NCSS 2007 for Windows (J. Hintze, Kaysville, UT), evaluated at $p < .05$.

EXPERIMENT 1: SOCIAL CONTINGENCY AND THE MALLEABILITY OF AUDITORY PREFERENCES IN NORTHERN BOBWHITE CHICKS

Given our desire to examine both interaction between combined pre- and post-natal exposure to a heterospecific auditory stimulus and the possible dependence of such interaction on the type of postnatal exposure received, we sought first to establish baseline responsivity of chicks to postnatal training in the absence of prenatal exposure. Based on the results of earlier studies (Harshaw et al., 2008; Lickliter & Hellewell, 1992; Lickliter & Lewkowicz, 1995; Lickliter & Virkar, 1989), we predicted that naïve chicks that receive no exposure to a maternal call prior to testing would show a significant preference for the BW over the JQ maternal call. We also expected to replicate the findings of Harshaw et al. (2008), and thus predicted both that brief contingent (CON) exposure to the heterospecific JQ call would significantly enhance chick preferences for that call compared to naïve subjects, and that chicks provided with yoked, non-contingent (YNO) exposure to the JQ call would continue to prefer the BW over the JQ call.

Method

Subjects. One hundred fifty-seven maternally naïve, incubator reared bobwhite chicks served as subjects. Chicks in the contingent condition (CON, $N = 69$) were trained and tested first. Chicks that failed to vocalize during CON training sessions ($N = 14$) were excluded from the study. Chicks in the yoked, noncontingent

Table 1. Preferences for the Japanese and Bobwhite Quail Maternal Calls in Experiment 1

Condition	<i>n</i> Responding	Preference		
		Japanese	Bobwhite	NP
Naïve	37	4	26**	7
Contingent JQ	40	14	18	8
Yoked JQ	40	9	25*	6

Note: All chicks were tested at 48 hr of age. NP, no preference.

* $p < .0005$.

** $p < .00001$.

condition (YNO, $N = 55$) were yoked to responding CON chicks. All remaining subjects ($N = 47$) served as naïve controls.

Procedure. All chicks in the CON conditions were provided with individual 5 min contingent exposures to the JQ maternal call on the day following hatching. During their training sessions, these chicks received a single playback of the maternal call following each contact vocalization they produced. Each subject in the YNO condition was yoked individually to a chick in the CON condition, and thus received the same amount of exposure to the maternal call, but not dependent on their vocalizations. Approximately 24 hr after training (on Day 2), all chicks were individually provided with a simultaneous choice test between the JQ and BW maternal calls. Naïve control subjects received no exposure to either maternal call prior to testing.

Results and Discussion

The preferences of chicks from all conditions are displayed in Table 1. Naïve bobwhite chicks displayed a species-specific preference for the BW over the JQ maternal call, $\chi^2(2, N = 37) = 23.1$, $w = .79$, $p < .00002$, despite having received no exposure to either call prior to testing. These chicks also displayed significantly longer duration scores ($z = -4.1$, effect size = $.77$, $p < .00005$) and shorter latencies of approach ($z = 3.36$, effect size = $.63$, $p < .0005$) for the BW than the JQ maternal call (see Fig. 1). In contrast, chicks provided with 5 min CON exposure to the JQ call failed to show a preference for the BW over the JQ call, $\chi^2(2, N = 40) = 3.8$, $w = .31$, $p = .15$, and also showed no significant difference in their duration ($z = -.23$, effect size = $.04$, $p = .819$) or latency ($z = 1.42$, effect size = $.26$, $p = .154$) scores for the two calls. Between-group comparisons of PTD and PTTA difference scores revealed that CON chicks displayed a significant difference in their duration but not latency scores for the JQ call compared to naïve controls ($Z = -2.39$, effect size = $.32$, $p = .008$; $Z = 1.53$, effect size = $.20$, $p = .063$, respectively). Chicks provided with

YNO exposure to the JQ call, on the other hand, continued to display the species-typical preference for the BW over the JQ maternal call, $\chi^2(2, N = 40) = 15.7$, $w = .63$, $p < .0005$. These chicks spent significantly more time in close proximity to the BW than the JQ call ($z = -2.37$, effect size = $.43$, $p < .009$) and also showed a tendency toward shorter latencies of approach to the bobwhite over the JQ maternal call ($z = 1.63$, effect size = $.30$, $p = .052$). In addition, these chicks showed no difference in their duration or latency scores for the JQ call compared to naïve chicks ($Z = -1.1$, effect size = $.15$, $p = .27$; $Z = 1.1$, effect size = $.04$, $p = .28$, respectively).

These results replicate the finding that brief contingent exposure to a heterospecific maternal call can significantly modify the auditory preferences displayed by bobwhite hatchlings (Harshaw et al., 2008). Whereas naïve bobwhite chicks showed the predicted species-specific preference for the maternal call of their own species over a heterospecific Japanese quail maternal call, bobwhite chicks that received contingent exposure to the JQ call failed to show a preference for the BW maternal call over the JQ maternal call. Chicks provided with yoked non-contingent exposure to the JQ call, on the other hand, continued to prefer the BW maternal call over the JQ

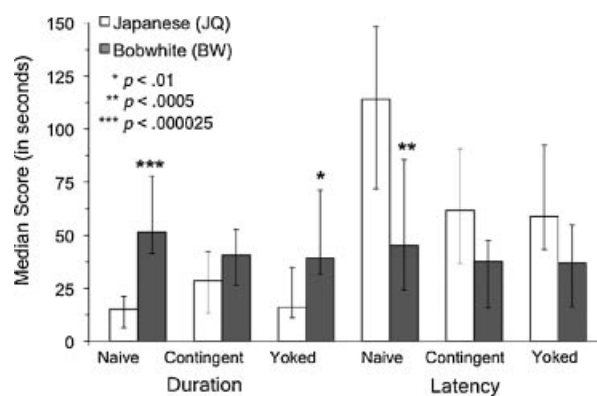


FIGURE 1 Median duration and latency scores ($\pm 95\%$ CI) for the Japanese and bobwhite quail maternal calls in Experiment 1. Significance indicated is for Wilcoxon matched-pairs signed-ranks tests.

maternal call in simultaneous choice tests, indicating the significance of contingent exposure to stimuli for postnatal auditory learning.

EXPERIMENT 2: EFFECTS OF MODIFIED PRENATAL AUDITORY EXPERIENCE ON SPECIES-TYPICAL AUDITORY PREFERENCES IN NORTHERN BOBWHITE CHICKS

Given our interest in the effects of prenatal sensory experience on postnatal learning, we next assessed the effects of brief prenatal exposure to a heterospecific maternal call on the subsequent postnatal responsiveness of hatchlings to that stimulus. We reasoned that prenatal exposure to the heterospecific Japanese quail call would result in perceptual learning that might influence or bias the postnatal acquisition of preferences for that call. Based on previous results demonstrating that prenatal sensory experience can influence postnatal attentional biases in bobwhite chicks (Honeycutt & Lickliter, 2002), we predicted that chicks provided with exposure to the JQ call prenatally would show a preference for the JQ over the BW maternal call following the same postnatal contingent exposure employed in Experiment 1. Given the results of Experiment 1, we also expected that chicks provided with CON exposure to the JQ call following prenatal exposure to that call would show greater preferences for the JQ call than chicks provided with YNO exposure following prenatal exposure to the JQ call.

Method

Subjects. One hundred fifty maternally naïve, incubator reared bobwhite chicks served as subjects. As was the case in Experiment 1, chicks in the CON condition ($N = 63$) were trained and tested first. Chicks that failed to vocalize during CON training sessions ($N = 9$) were excluded from the study. Chicks in the YNO condition ($N = 54$) were individually yoked to responding CON chicks. All remaining chicks ($N = 42$) served as controls.

Procedure. The procedures and postnatal conditions were identical to those employed in Experiment 1, with the exception that all chicks in the current experiment were exposed passively to the JQ maternal call as embryos for 5 min/hr over the course of their last 12 hr of incubation. We deliberately employed a small amount of prenatal auditory stimulation (60 min total) compared to previous studies (240 min of total exposure, see Lickliter & Hellewell, 1992; Lickliter et al., 2002), as we were interested in the possible additive or synergistic effects of combined prenatal and postnatal stimulation on the development of preferences for the heterospecific auditory stimulus.

Results and Discussion

The 60 min prenatal exposure to the JQ call had no obvious effect on the auditory preferences of chicks provided with no subsequent exposure to the call prior to testing at 48 hr of age. As can be seen in Table 2, chicks provided with only prenatal exposure to the JQ call showed a significant preference for the BW over the JQ maternal call, $\chi^2(2, N = 37) = 38, w = 1.01, p < .000001$. These chicks had significantly longer duration scores ($z = -4.1$, effect size = .86, $p < .00001$) and shorter latencies of approach ($z = 3.04$, effect size = .57, $p < .002$) for the BW than the JQ maternal call (see Fig. 2). These chicks also showed PTD and PTTA difference scores that were not significantly different from those of the chicks in Experiment 1 who received no exposure to the JQ call prior to testing ($Z = -1.49$, effect size = .2, $p = .137$; $Z = .29$, effect size = .04, $p = .775$, respectively).

Chicks provided with both pre- and postnatal exposure to the JQ call, on the other hand, showed evidence of having been affected by the prenatal exposure. Those provided with 60 min prenatal and 5 min postnatal CON exposure to the JQ call showed a significant preference for the JQ over the BW maternal call, $\chi^2(2, N = 36) = 10.2, w = .53, p < .007$. These chicks displayed significantly higher duration scores ($z = 2.06$, effect size = .5, $p < .005$)

Table 2. Preferences of Chicks Exposed to the Japanese Quail Maternal Call Prenatally in Experiment 2

Postnatal Exposure	<i>n</i> Responding	Preference		
		Japanese	Bobwhite	NP
None	37	3	30**	4
Contingent JQ	36	21*	7	8
Yoked JQ	38	18	12	8

Note: All chicks were tested at 48 hr of age. NP, no preference.

* $p < .007$.

** $p < .000001$.

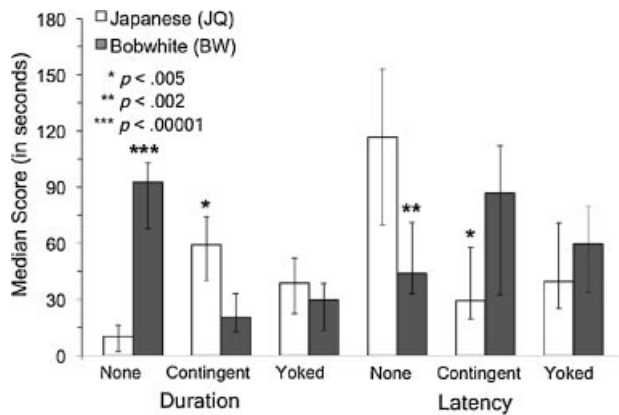


FIGURE 2 Median duration and latency scores ($\pm 95\%$ CI) for the Japanese and bobwhite quail maternal calls in Experiment 2. All chicks received 60 min prenatal exposure to the JQ call and are classified with respect to the postnatal exposure they received. Significance indicated is for Wilcoxon matched-pairs signed-ranks tests.

and shorter latency of approach ($z = 2.7$, effect size = .52, $p < .004$) for the JQ than the BW maternal call. In contrast, chicks provided with 60 min prenatal and 5 min postnatal YNO exposure to the JQ call failed to show a preference for either call during testing, $\chi^2(2, N = 38) = 4.0$, $w = .32$, $p = .153$, and also showed no significant differences in their duration ($z = 1.33$, effect size = .25, $p = .092$) or latency ($z = 1.23$, effect size = .23, $p = .11$) scores for the two calls.

Between-group comparisons revealed that, irrespective of the type of postnatal exposure they received (contingent vs. yoked), chicks provided with combined prenatal and postnatal exposure to the JQ maternal call showed a significant increase in PTD scores for the JQ call compared to chicks in Experiment 1 (see Fig. 3), who received the same type of postnatal but no prenatal exposure to the JQ call ($Z = 1.79$, effect size = .24, $p = .037$; $Z = 2.63$, effect size = .31, $p < .01$, respectively). The same was true of these chicks' latency (PTTA difference) scores for the JQ call. Chicks that received 60 min prenatal plus either postnatal CON or YNO exposure to the JQ call showed significantly shorter latency scores for JQ call compared to chicks that received no prenatal exposure to the call ($Z = -2.82$, effect size = .38, $p < .003$; $Z = -1.93$, effect size = .25, $p = .027$, respectively). However, contrary to our expectations, chicks provided with CON exposure did not show significantly higher duration or shorter latency scores for the JQ call than chicks provided with YNO exposure to the call ($Z = .7$, effect size = .1, $p = .241$; $Z = -1.27$, effect size = .17, $p = .102$, respectively).

These results indicate that relatively brief (60 min) prenatal exposure to a heterospecific Japanese quail maternal call can significantly influence the responsivity

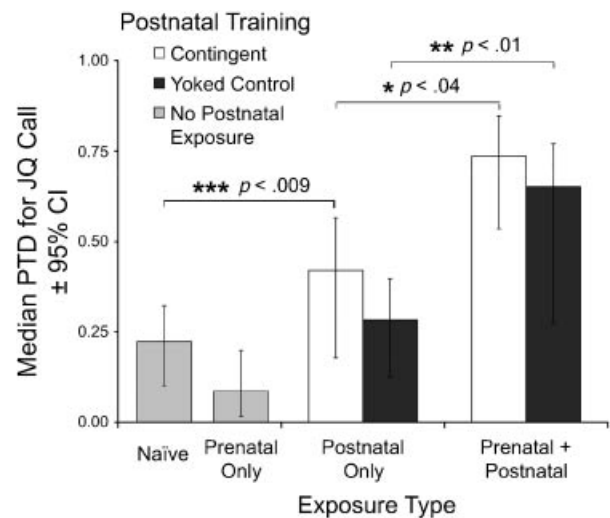


FIGURE 3 Median proportion of total duration (PTD) scores ($\pm 95\%$ CI) for the Japanese quail call for all subjects from Experiments 1 and 2. A PTD score of .5 indicates no preference for either call. Significance indicated is for Mann-Whitney U tests.

of hatchlings to a 5 min postnatal exposure to the same call, whether or not the postnatal exposure is contingent on the behavior of chicks. Importantly, chicks that received only 60 min prenatal and no postnatal exposure to the JQ call showed duration and latency scores that did not differ significantly from those of naïve chicks who received no exposure to the JQ call prior to testing. These results suggest that prenatal exposure to the JQ call resulted in some form of perceptual learning that biased chicks to be more responsive to that call following hatching.

One possibility is that the chicks that received prenatal exposure to the JQ call were more responsive during their postnatal training sessions, vocalizing more and thus hearing the call more frequently than chicks who received no prior exposure. However, the mean number of times chicks vocalized during CON training in Experiments 1 and 2 (34.2 ± 2.5 and 32.5 ± 3.6 , respectively) did not differ ($t = .72$, $p = .472$).¹ The mean number of playbacks of the maternal call chicks received during CON training in Experiment 2 (39.5 ± 2) was higher than that for Experiment 1 (36.6 ± 2.2), but the difference was short of significance ($t = 1.9$, $p = .056$), suggesting that chicks may have initially been slightly *less* responsive during training in Experiment 2, requiring more non-contingent presentations at the onset of training.

Another possibility is that the chicks that received prenatal exposure to the JQ call experienced a transient

¹This comparison involved only 20 of the 54 subjects given CON training in Experiment 2, as the program used for training did not initially record contingent and noncontingent stimulus presentations separately.

boost in their attraction to that call that affected their responsiveness to training at 24 hr of age but decayed by testing at 48 hr. The purpose of the next experiment was to examine this possibility, by measuring the preferences of prenatally exposed and naïve chicks at 24 rather than 48 hr following hatch.

EXPERIMENT 3: THE EFFECTS OF PRENATAL EXPOSURE TO A HETEROSPECIFIC CALL ON POSTNATAL AUDITORY PREFERENCES OF BOBWHITE CHICKS

The purpose of this experiment was to determine the effects of brief prenatal exposure to the heterospecific JQ maternal call on the preferences of BW chicks for that call at the same age (24 hr old) at which chicks received contingent training in Experiments 1 and 2. Given the small amount of prenatal stimulation employed (60 min total) and the results of Experiment 2, we predicted that prenatally exposed chicks would not show a significant difference in their approach behavior toward the JQ call relative to the BW call in simultaneous choice tests when compared to unexposed control chicks.

Method

Subjects. Ninety-six maternally naïve, incubator reared bobwhite chicks served as subjects. Embryos were either exposed to the JQ call for 5 min/hr during their last 12 hr of incubation ($N = 43$) or received no modified prenatal stimulation ($N = 53$).

Procedure. The procedures were identical to those employed in the first two experiments, with the exception that chicks received no postnatal exposure to the JQ call. All chicks were provided with a simultaneous choice test between the JQ and BW maternal calls at 24 hr following hatching.

Results and Discussion

As can be seen in Table 3, both unexposed and prenatally exposed chicks showed a significant preference for the

BW over the JQ maternal call at 24 hr of age ($\chi^2(2, N = 43) = 53.9, w = 1.12, p < .000001$, and $\chi^2(2, N = 36) = 12.2, w = .58, p < .003$, respectively). Both groups of chicks also showed significantly longer duration ($Z = 5.02$, effect size = .88, $p < .000001$; $Z = 3.4$, effect size = .64, $p < .0008$, respectively) and shorter latency ($Z = 3.9$, effect size = .67, $p < .00007$; $Z = 1.7$, effect size = .33, $p < .05$, respectively) scores for the BW than the JQ call. However, between-group comparisons revealed that chicks prenatally exposed to the JQ call displayed significantly longer duration (PTD) and shorter latency (PTTA difference) scores for the JQ call than unexposed, naïve chicks ($Z = -1.77$, effect size = .23, $p < .04$; $Z = 2.7$, effect size = .35, $p < .004$, respectively; see Fig. 4).

These results suggest that 60 min of prenatal exposure to a heterospecific, JQ maternal call over the last 12 hr of incubation results in an increase in chicks' attraction and responsiveness to the JQ call at 24 hr of age compared to naïve, unexposed chicks. Given that such an increase in responsiveness to the JQ call was not seen at 48 hr of age (Experiment 2), it appears that the effects of prenatal exposure to the JQ call on postnatal preferences is relatively short-lived in the absence of additional postnatal exposure. However, this transient increase in chick responsiveness to the JQ call present soon after hatching appears to have been sufficient to foster the enhanced preference for the JQ call seen in chicks provided both prenatal and postnatal exposure in Experiment 2.

GENERAL DISCUSSION

This study confirms and extends the finding that bobwhite hatchlings provided the opportunity to interact with a contingently presented auditory stimulus—conditions that map far more closely onto the real-world developmental ecologies of precocial birds than traditional passive exposure paradigms—very rapidly acquire or show a significant enhancement of their preference for that stimulus (Harshaw & Lickliter, 2007; Harshaw et al., 2008). A single 5 min postnatal contingent exposure to a heterospecific Japanese quail maternal call was

Table 3. Preferences of Postnatally Unexposed Chicks Tested at 24 hr of Age in Experiment 3

Prenatal Exposure	<i>n</i> Responding	Preference		
		Japanese	Bobwhite	NP
None (Naïve)	43	2	37**	4
60 min JQ	36	4	21*	11

Note: NP, no preference.

* $p < .003$.

** $p < .000001$.

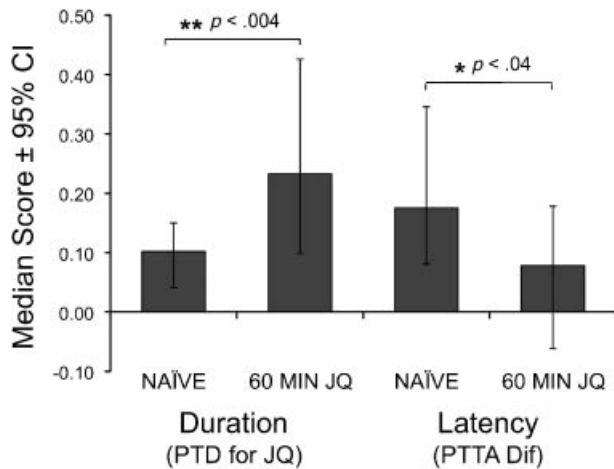


FIGURE 4 Median proportion of total duration (PTD) scores ($\pm 95\%$ CI) for the Japanese quail call and PTTA difference (JQ – BW) scores for all subjects from Experiment 3. A PTD score of .5 and/or a PTTA difference score of zero indicates no preference for either call. Significance indicated is for Mann–Whitney U tests.

sufficient to disrupt the normally robust preference of bobwhite chicks for the maternal call of their own species (Experiment 1). We hypothesized that chicks provided with a small amount of prenatal exposure to the JQ call would show enhanced preferences for the JQ call following subsequent postnatal training with the call compared to chicks lacking such prenatal experience. Confirming this prediction, prenatal exposure to the JQ maternal call for 5 min/hr over the course of the last 12 hr of incubation—a small amount of stimulation compared to previous studies of auditory learning in quail embryos and hatchlings (e.g., Lickliter & Hellewell, 1992; Lickliter et al., 2002)—significantly modified the postnatal responsivity of chicks to that call. Chicks provided with either contingent or yoked, non-contingent exposure to the JQ call following prenatal exposure showed significantly greater preferences for the JQ call at 48 hr of age (24 hr following training) than chicks who received postnatal exposure alone (Experiment 2). In contrast, chicks provided with prenatal but no postnatal exposure to the JQ call and tested at 48 hr of age preferred the bobwhite maternal call, as did unexposed, naïve chicks.

Across all of the conditions of the study, the only group of chicks that showed a significant preference for the JQ over the BW maternal call was that provided with both 60 min passive prenatal and 5 min contingent postnatal exposure to the JQ call. This finding confirms the main prediction of our study, highlighting both the strong influence of contingently encountered social stimuli on the acquisition of filial preferences (cf. Harshaw & Lickliter, 2007; ten Cate, 1989) and the salience of the

transnatal continuity of socially derived stimuli (Bertin et al., 2010; Fifer & Moon, 1994; Honeycutt & Alberts, 2005). It is important to note that the effect of contingent compared to yoked, non-contingent exposure on chicks' preference scores was small (and statistically insignificant in the current study) compared to the large effect of combined prenatal and postnatal exposure. The prenatal exposure used in the present study clearly influenced some aspect(s) of chicks' attraction or responsivity to the JQ call during postnatal training. Based on the available training data, this result did not appear to be due to chicks simply being more responsive behaviorally (i.e., vocalizing more) during their training sessions. The prenatal exposure to the heterospecific JQ call thus likely resulted in some form of perceptual learning that biased or "primed" chicks to respond differentially in subsequent encounters with that familiar stimulus.

The results of Experiment 3, in which chicks provided with prenatal exposure to the JQ call showed significantly greater duration and latency scores for the call than unexposed chicks when tested at 24 hr (instead of 48 hr) of age, suggest that there was a transient boost in the relative attractiveness/salience of the call following prenatal exposure. This appeared to affect how chicks responded to the call during their training sessions at 24 hr following hatching (facilitating perception, attention and/or memory), but was no longer detectable by 48 hr of age. Thus, additional postnatal experience appears to be necessary for the maintenance of perceptual sensitivities induced by modified prenatal experience. Chicks in Experiment 2 that were exposed prenatally to the JQ call but received no postnatal exposure showed no significant differences in their behavior from unexposed chicks when tested at 48 hr following hatching.

An important limitation of the current study is the use of only a single heterospecific stimulus for prenatal and postnatal exposures and only single exemplars of the conspecific and heterospecific calls for simultaneous choice testing. This a consequence both of the tradition and constraints of simultaneous choice testing of filial auditory preferences in precocial birds (see Gottlieb, 1971) and limited supply of available exemplars, particularly of maternal stimuli (e.g., in the archive of the Cornell Lab for Ornithology). Future studies will thus be needed to test the generality of the effects observed in the current study, both within and across species. There are also a number of interesting hypotheses that remain to be explored, particularly with respect to potential constraints on the malleability of species-typical social preferences. For example, some precocial birds species may have evolved greater "defenses" against susceptibility to the calls of related species with overlapping as opposed to non-overlapping geographical ranges. There are also questions of mechanism that remain

unexplored. For example, what specific neurological changes are induced by prenatal auditory stimulation (e.g., Chaudhury, Nag, & Wadhwa, 2006; Markham, Shimizu, & Lickliter, 2008) and how such changes relate to the differences in postnatal learning observed in the current study.

The present study, although subject to limitations described above, adds to a growing body of evidence from birds and mammals illustrating the influence of prenatal experience on subsequent perceptual, motor, and social development (e.g., Casey & Lickliter, 1998; DeCasper & Spence, 1986; DiPietro, 2004; Fifer & Moon, 1994; Honeycutt & Alberts, 2005; Jaime & Lickliter, 2006; Reynolds & Lickliter, 2004). Our results indicate that even a relatively small amount of prenatal exposure to a specific auditory stimulus can have a significant influence on the avian neonate's postnatal auditory preferences. Species-specific auditory experiences during the prenatal period are part of the normal developmental context of many precocial birds (e.g., Gottlieb, 1971; Tuculescu & Griswold, 1983) as well as humans (e.g., Fifer & Moon, 1994, 1995; Kisilevsky et al., 2003). From a developmental perspective, the specific experiences and interactions that make up the young organism's developmental context play a key role in the development and maintenance of its species-typical behavior (see Haraway & Maples, 1998; Kaufman, 1975; Lickliter, 2000; Miller, 1997; West, King, & White, 2003). On the other hand, alterations or modifications to normally occurring experiences and interactions can be the basis for the generation of novel behavior ("behavioral neophenotypes", see Johnston & Gottlieb, 1990; Kuo, 1967). Novel behaviors brought on by alterations in species-typical prenatal and/or postnatal environments can in turn lead to other behavioral changes, including diet, habitat use, and patterns of social behavior (Gottlieb, 1992; Lickliter & Harshaw, 2010).

Our demonstration of the rapid redirection of the normally robust species-specific auditory preferences of bobwhite quail chicks suggests a dynamic interplay between the experiential forces that foster species-typical behavior and those capable of generating novel behaviors during early development. This interplay—between factors that serve to canalize behavioral phenotypes and those that foster behavioral malleability—appears particularly evident during early development, when neural, physiological, perceptual, and behavioral systems are undergoing rapid change and reorganization (Lickliter & Harshaw, 2010). An important next step in the study of the origins of species-typical biases or perceptual predispositions will be to develop cross-level frameworks that can link and model the interactive, bidirectional processes occurring at these different levels of analysis over individual ontogeny.

NOTES

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