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Stimulus Contingency and the Malleability of Species-Typical Auditory Preferences in Northern Bobwhite (*Colinus virginianus*) Hatchlings

ABSTRACT: *Precocial avian hatchlings are typically highly social and show strong species-typical preferences for the maternal calls of their own species. The influence of social contingencies on the acquisition of species-specific preferences has, however, largely been neglected. We found that exposing bobwhite (BW) quail chicks to a Japanese quail (JQ) call contingent on their own vocalizations for 5 min was sufficient to eliminate their species-typical preference for the BW maternal call. Yoked, noncontingent exposure had no such effect. The introduction of variability to the contingency, but not a lengthening of the training session, was found to engender even higher preferences for the JQ call. Chicks provided with contingent exposure to the JQ call on a variable ratio schedule showed a significant preference for the JQ over the BW maternal call, whereas chicks provided with equivalent fixed ratio exposure did not. These results highlight the role that social interaction and contingency can play in the acquisition and maintenance of species-specific auditory preferences in precocial avian species. © 2008 Wiley Periodicals, Inc.* Dev Psychobiol 50: 460–472, 2008.

Keywords: *contingency; variability; filial imprinting; auditory preferences; malleability; schedules of reinforcement; perceptual development; Northern bobwhite*

INTRODUCTION

Normally occurring sensory experience has been shown to have a powerful canalizing influence on perceptual and behavioral development. In a classic series of studies Gottlieb (1971) demonstrated that the strong species-specific auditory preferences of ducklings were due in large part to the canalizing influence of normally occurring prenatal auditory experience, particularly exposure to embryonic vocalizations. Gottlieb (1987, 1991a) further demonstrated that the species-typical preferences of ducklings for the maternal call of their own species could be rendered malleable by altering the amount of prenatal exposure that they received to their own and their siblings' embryonic vocalizations. Gottlieb (1991b, 1993) also showed that the species-specific auditory preferences of ducklings could be rendered malleable by rearing ducklings socially and/or with tactile stimulation rather than in isolation following hatch. Ducklings reared socially (1991b) or with alternative sources of tactile stimulation (1993) and exposed to a species-atypical chicken maternal call over several days showed significant preferences for the chicken call, whereas ducklings reared in social isolation did not.

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Based on such findings, Gottlieb (1991b) proposed that the ''canalization'' of behavior and resulting decrease in plasticity or malleability over the course of early development was the result of the young organism's range of usual or typical experiences within their species-typical developmental system or niche. Gottlieb argued that such species-typical experience fostered the development of species-specific behavior, preventing embryos, and hatchlings from being susceptible to non species-typical forms of stimulation. Apart from Gottlieb's pioneering work, few studies have explored the conditions that might precipitate inter-specific malleability or buffer young organisms from acquiring species-atypical perceptual preferences during early development.

An examination of the normally occurring sources and types of sensory stimulation available to most precocial avian species reveals the presence and likely importance of social interaction during their early development (e.g., Collias, 1952, 2000; Lickliter, 1989, 2005; Lickliter & Gottlieb, 1985; Lickliter, Dyer, & McBride, 1993; McBride, Parer, & Foenander, 1969). The majority of such species are highly social and a number of studies have revealed that interaction between same-age broodmates and between adults and young begins even prior to hatch in many species (Hess, 1972; Johnson, 1969; Norton-Griffiths, 1969; Tschanz, 1968; Tuculescu & Griswold, 1983; Vince, 1972).

The majority of studies examining the early acquisition of auditory preferences in precocial birds have nonetheless employed passive or noncontingent exposure of embryos and hatchlings to auditory stimuli. Studies of the Northern bobwhite quail (*Colinus virginianus*), for example, have shown that bobwhite (BW) chicks require 240–480 min of passive exposure to an individual BW maternal call to show a significant preference for that call over an unfamiliar call (Foushée & Lickliter, 2002; Lickliter & Hellewell, 1992). Gottlieb (1971) similarly employed passive, noncontingent exposure of ducklings and embryos to auditory stimulation in his studies of the development and malleability of species-specific auditory preferences. Gottlieb (1987, 1991a) reported that vocal mallard ducklings require 11–30 hr of exposure to a chicken call to show a disruption of their normal preference for the mallard over the chicken maternal call. A number of studies have, however, pointed to a potentially strong influence of contingency on the development of filial preferences in precocial avian species (e.g., Bateson & Reese, 1969; Evans, 1991; Harshaw & Lickliter, 2007; Johnson, Bolhuis, & Horn, 1985; ten Cate, 1989b). Harshaw and Lickliter (2007), for example, recently demonstrated that providing day-old BW chicks with as little as 5 min of exposure to a vocal-auditory contingency, in which an individual BW maternal assembly call was played each time the chick vocalized, was sufficient to engender significant preferences for the familiarized over a novel BW maternal call. These preferences were established with 1% or less of the exposure to the maternal call required in previous studies employing passive exposure to the same calls (Foushée & Lickliter, 2002; Lickliter & Hellewell, 1992).

Given that social interaction and social contingencies appear to have an influence on the early perceptual development of many precocial birds (e.g., Collias, 1952, 2000; ten Cate, 1989a; Tuculescu & Griswold, 1983), we thought it plausible that contingency could provide one mechanism through which species-specific auditory preferences might become more malleable during early development. The Northern BW is a precocial avian species that typically establishes regular vocal contact with parents and broodmates prior to or soon after hatch (Stokes, 1967; Vince, 1972). BW hatchlings also typically exhibit strong species-specific preferences for the BW maternal call over the maternal calls of other species shortly after hatch (Banker & Lickliter, 1993; Heaton & Gallaher, 1981; Heaton, Miller, & Goodwin, 1978; Lickliter & Virkar, 1989). These features make the BW an excellent model for studying early social influences on the development and malleability of species-typical auditory preferences. In the current study we explored whether brief contingent exposure to a heterospecific (species-atypical) maternal call could significantly shift the normally robust species-specific auditory preferences of BW hatchlings.

GENERAL METHOD

Several features of our method were common across all experiments of the study and are discussed first.

Subjects

Fertile, unincubated BW 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 before hatch, embryos were transferred to a Grumbach S84 Hatcher, maintained at 37.5°C and 80% relative humidity. Shortly after hatch, chicks were transferred to a sound-proof rearing room and placed in groups of 10–15 same-aged chicks to mimic typical brood conditions for BWs (Stokes, 1967). These groups were housed in large plastic tubs (25 cm wide × 15 cm high × 45 cm long) placed on shelves in a Nuaire Model NU-605-500 Animal Isolator (Plymouth, MN). Ambient air temperature was maintained at approximately 35.5°C in the rearing room (−.5°C per day post-hatch) and between 29.5 and 32.8°C in the training/testing room. Chicks thus experienced little or no thermal distress during their training and testing sessions. Food and water were available ad libitum while chicks were in the rearing room. Chicks for each condition were drawn from 2 or more weekly batches to minimize the influence of any inter-batch variability on the study.

Apparatus

All training and testing sessions were conducted in a large circular arena (dia = 130 cm, height = 24 cm) within a sound-attenuated room, nonadjacent 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 on the ceiling above the arena, and a microphone, placed beneath the arena, provided continuous, visual and auditory access to all 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 (B & K Instruments, Marlborough, MA). 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 beginning of stimulation and/or data collection. All stimulus deliveries and behavioral observations were made using Visual Basic/Excel programs.

Auditory Stimuli

The auditory stimuli used during training and testing sessions throughout the study were a Japanese quail (JQ, *Coturnix japonica*) maternal call (Long, Kennedy, & Balaban, 2001; Park & Balaban, 1991) and a BW quail maternal call (Call B; Heaton et al., 1978), both cleaned of background noise by The Borror Laboratory of Bioacoustics (Columbus, OH). These calls are functionally similar, both being maternal assembly calls for their respective species, but differ in structural and frequency characteristics. The BW 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 JQ maternal call similarly consists of five notes, but is 1.8 s long, and has dominant frequencies of .75–.85 and 1.6–1.7 kHz.

Training Sessions

All training sessions were conducted on Day 1 (Day 0 being the day of hatch), approximately 24 hr following hatch, and involved individual exposures to either the heterospecific Japanese (JQ) or the conspecific BW quail maternal call. During contingent training sessions, presentation of the call was dependent upon chick distress/contact vocalization. BW chick distress/contact calls are easily distinguishable from other chick vocalizations, generally consisting of a string of rapid ‘‘peeps’’ (Stoumbos, 1990). Experimenters were instructed to play the call up to five times noncontingently to coax initially nonvocal chicks to vocalize (see Harshaw & Lickliter, 2007). Any chick failing to respond to this procedure was removed from the study. Presentations of the call were alternated and balanced across sides within-session to prevent the development of any side-biases in chicks. The precise 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, allowing for a fully yoked design. Yoked, noncontingent training sessions were identical to contingent training sessions except for the lack of systematic contingency between the chick’s behavior and the auditory stimuli being presented.

Testing Sessions

All testing sessions took place on Day 2 post-hatch, approximately 24 hr following training for all subjects but naïve controls (who received no training). Although this interval can be seen as relatively short, in a naturalistic setting chicks would undoubtedly experience far more than 5 min of social interaction with their mother during their first 48 hr post-hatch. The 24 hr retention interval was thus employed largely for the sake of comparing our results to those of other studies of the development of auditory preferences in precocial birds. Testing sessions were identical across conditions and experiments, consisting of 5-min simultaneous choice tests between the heterospecific JQ and conspecific BW quail maternal calls. Both calls were played at identical repetition rates from opposite sides of the arena for the duration of the test and were fully counterbalanced within condition. A semicircular approach area, representing approximately 5% of the total surface area of the arena, was demarcated around each speaker on a monitor used by experimenters for observing sessions. Upon entry into one of these approach areas the experimenter clicked on one of two buttons on a Visual Basic program. The button was held down until the chick exited the approach area. This method provided tallies of entries into both areas, cumulative scores for duration of time spent within each approach area, and scores for latency of approach.

Data Analyses

Raw duration scores were converted into categorical ‘‘preferences’’ so that Chi-square tests could be performed on their distributions. Following the convention employed in a number of previous studies (e.g., Heaton et al., 1978; Lickliter & Hellewell, 1992), chicks failing to spend at least 10 s in an approach area were scored as nonresponders 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 scored as displaying a preference for a call if the chick spent at least 10 s in the approach area for that call and at least twice as long in that 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. Nonparametric tests were employed because the data for many of our conditions did not meet the assumption of normality required for parametric testing. Chi-square tests were supplemented with Wilcoxon matched-pairs signed-ranks tests on raw latency and duration scores. Duration and latency scores were also 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} minus 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: CONTINGENCY AND THE MALLEABILITY OF AUDITORY PREFERENCES IN NORTHERN BOBWHITE NEONATES

The purpose of this experiment was to verify the presence of species-specific auditory preferences for their conspecific maternal call in naïve BW chicks (e.g., Banker & Lickliter, 1993; Lickliter & Virkar, 1989) and to examine the effects of brief, contingent exposure to either a conspecific or heterospecific quail call on such species-typical preferences. We predicted that naïve chicks would show a strong preference for the BW over a JQ maternal call, that contingent (CON) exposure to the JQ call would significantly enhance preferences for that heterospecific call and that chicks given yoked, noncontingent (NOC) exposure to the JQ call would show no such shift in their preferences. We also hypothesized that chicks provided with CON exposure to the BW call would show increased preferences for that call over the JQ call compared to naïve chicks.

Method

Subjects. One hundred sixty-four maternally naïve, incubator reared BW chicks served as subjects. Chicks in the CON conditions ($N = 43$ for JQ, $N = 37$ for BW) were trained and tested first. Chicks that failed to vocalize during these training sessions ($N = 5$ for JQ, $N = 5$ for BW) were excluded from the study. Yoked subjects were not run for the BW call given that a significant shift in preference was not found for CON BW chicks (see below). Chicks in the NOC JQ condition ($N = 38$) were yoked to responding CON JQ chicks. All remaining subjects ($N = 46$) served as naïve controls.

Procedure. All chicks in the CON conditions were given individual 5-min contingent exposures to either the JQ or BW maternal call on a fixed 1:1 ratio (FR1) schedule on Day 1 post-hatch. That is, chicks received a single playback of the maternal call for each contact vocalization emitted during their training sessions. Each subject in the NOC JQ condition was individually yoked to a chick in the CON JQ condition. Naïve subjects received no exposure to either maternal call prior to testing. All subjects were tested approximately 24 hr later (on Day 2) in individual simultaneous choice tests between the JQ and BW maternal calls.

Results and Discussion. Chick preferences are displayed in Table 1. Confirming the results of previous studies, naïve BW chicks displayed a strong species-specific preference for the BW maternal call when tested 2 days post-hatch, $\chi^2(2,\ N = 40) = 24.8,\ w = .79,\ p < .000005$. These chicks had significantly longer duration scores ($z = -3.94$, effect size $= .71$, $p < .0001$) and significantly shorter latencies of approach ($z = 2.8$, effect size $= .51$, $p < .005$) to the BW than the JQ maternal call (see Fig. 1).

Chicks given 5-min CON exposure to the JQ maternal call no longer showed a preference for the BW call, $\chi^2(2,\ N = 37) = .05,\ w = .04,\ p = .973$. These chicks showed no difference in duration ($z = .37$, effect size $= .07$, $p = .712$) or latency ($z = .16$, effect size $= .03$, $p = .874$) scores between the two maternal calls. Chicks given yoked, noncontingent exposure to the JQ call, on the other hand, displayed the species-typical preference for the BW maternal call, $\chi^2(2,\ N = 31) = 8.97,\ w = .54,\ p < .0125$. These chicks showed shorter latencies of approach to the BW over the JQ maternal call ($z = 2.67$, effect size $= .55$, $p < .005$) and duration scores that approached a significant difference between the two calls in favor of the BW call ($z = -1.63$, effect size $= .33$, $p = .053$).

Chicks given 5-min CON exposure to the JQ call showed significantly larger duration (PTD) scores ($z = 3.25$, effect size $= -.43$, $p = .0006$) and significantly shorter latency (PTTA difference) scores ($z = -1.93$, effect size $= .26$, $p = .027$) for the JQ call than naïve chicks (see Fig. 2). Chicks given 5-min yoked exposure to the JQ call, in contrast, showed significantly shorter duration scores ($z = -2.41$, effect size $= .34$, $p = .008$) and significantly longer latency scores ($z = 2.32$, effect size $= -.33$, $p = .01$) for the JQ call than chicks given CON exposure to the JQ call. Yoked chicks also showed no difference in either duration ($z = -.25$, effect size $= .03$, $p = .803$) or latency ($z = .58$, effect size $= -.08$, $p = .562$) scores for the JQ call from naïve chicks.

Chicks given 5-min CON exposure to the BW call showed significant preferences for the BW call, $\chi^2(2,\ N = 31) = 32,\ w = 1.02,\ p < .000001$, and significantly larger duration ($z = -4.14$, effect size $= .85$, $p < .00002$) and shorter latency ($z = 2.82$, effect size $= .58$, $p < .003$) scores for the BW than the JQ call. These chicks, however, showed no significant difference in duration ($z = 1.32$,

Table 1. Preferences for the Japanese and Bobwhite Quail Maternal Calls in Experiments 1 and 2

		Preference		
Condition	*n* Responding	Japanese	Bobwhite	NP
Experiment 1				
Naïve	40	4	28****	8
5-min BW CON	31	1	25****	5
5-min JQ CON	37	12	13	12
5-min JQ yoked	31	8	18**	5
Experiment 2				
8-min BW CON	32	5	22***	5
10-min BW CON	31	3	23****	5
8-min JQ CON	31	10	13	8
8-min JQ yoked	31	2	21**	8
10-min JQ CON	34	4	16	14
10-min JQ yoked	29	4	17*	8

NP, no preference, CON, contingent.
*$p < .05$.
**$p < .0125$.
***$p < .0005$.
****$p < .00001$.

effect size = −.18, $p = .185$) or latency ($z = .85$, effect size = −.12, $p = .397$) scores from naïve chicks. This finding suggests that naïve BW chicks may be at or very near a ceiling in their preferential responding to the BW over the JQ call, as measured in this study.

The results of this experiment confirmed our prediction that brief contingent exposure to a heterospecific call would significantly shift the species-typical preferences of BW hatchlings. We found that a single 5-min contingent exposure to the JQ maternal call was sufficient to eliminate BW chicks' normally strong preference for the maternal call of their own species, whereas yoked exposure had no effect on chick preferences. This is an impressive finding in light of previous results investigating the malleability of species-specific auditory preferences in precocial birds. Gottlieb (1987, 1991a), for example, had to expose duckling embryos and hatchlings to a chicken maternal call for 11–30 hr to achieve results similar to those of the present study. By devocalizing ducklings, however, Gottlieb was able to achieve a higher degree of malleability, completely redirecting the species typical preferences of these birds toward a heterospecific maternal call with 11–30 hr of exposure to that call. Given

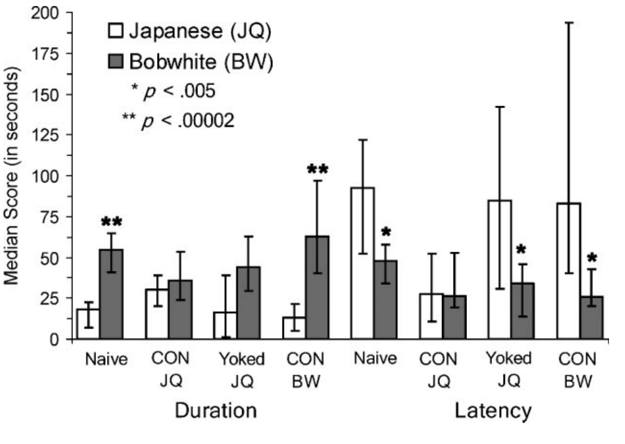

FIGURE 1 Median duration and latency scores (±95% CI) for the Japanese and bobwhite quail maternal calls for Experiment 1. Significance indicated is for Wilcoxon matched-pairs signed-ranks tests.

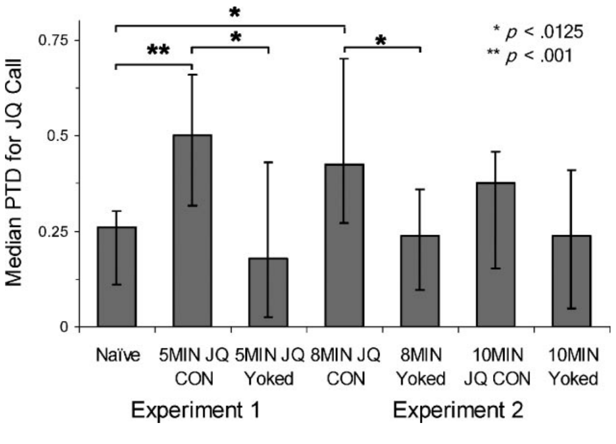

FIGURE 2 Median proportion of total duration (PTD) scores (±95% CI) for the Japanese quail call for naïve subjects and subjects exposed to the JQ call in Experiments 1 and 2. A PTD score of .5 indicates no preference for either call. Significance indicated is for Mann–Whitney *U* tests.

that the 5-min contingent exposure employed in the present experiment was sufficient to achieve an elimination but not reversal of species-typical preferences in BW chicks, we were interested in whether increasing the overall amount of contingent exposure to the heterospecific call would further increase the preferences of BW chicks for that call. We were also interested in whether increasing the amount of contingent exposure to the BW maternal call would raise preferences for that call significantly above the levels displayed by naïve chicks.

EXPERIMENT 2: EFFECTS OF EXPOSURE DURATION ON THE MALLEABILITY OF AUDITORY PREFERENCES IN NORTHERN BOBWHITE NEONATES

The purpose of this experiment was to examine the effects of the length of a contingent training session on the acquisition of auditory preferences for a conspecific or heterospecific maternal call in BW chicks. We predicted that lengthening the exposure of BW chicks to a vocal-auditory contingency would produce a further increase in preferences for the JQ call in chicks given contingent exposure to the JQ call and that chicks given yoked, noncontingent exposure to the JQ call would show no change in their auditory preferences. It was also hypothesized that a lengthening of BW contingent training sessions would produce a further increase in preferences for the BW over the JQ maternal call.

Methods

Subjects. Two hundred forty-five maternally naïve, incubator reared BW chicks served as subjects. Chicks in the 8- and 10-min contingent conditions ($N = 48$ and $N = 47$, respectively, for JQ and $N = 44$ and $N = 40$ for BW) were trained first and all nonresponders were excluded from later testing ($N = 16$ for 8-min JQ, $N = 13$ for 10-min JQ, $N = 10$ for 8-min BW, and $N = 7$ for 10-min BW sessions). Yoked controls were not run for CON BW chicks because of the small magnitude of increase in preferences observed in these conditions (see below). Chicks in the 8- and 10-min NOC JQ conditions ($N = 32$ and $N = 34$, respectively) were later yoked to responding CON JQ chicks.

Procedure. Chicks were given either 8- or 10-min individual contingent (FR1) exposures to the JQ or BW maternal call on Day 1 post-hatch. Each subject in a NOC condition was yoked individually to a chick in the corresponding CON condition. As in the previous experiment, all subjects were tested approximately 24 hr later in individual simultaneous choice tests between the JQ and BW maternal calls.

Results and Discussion

As can be seen in Table 1, chicks given 8-min CON exposure to the JQ call showed no preference for either maternal call, $\chi^2(2,\ N = 32) = 1.23$, $w = .20$, $p = .542$. These chicks showed no difference in duration ($z = -.39$, effect size = .08, $p = .695$) or latency ($z = -1.12$, effect size = .23, $p = .264$) scores between the JQ and BW calls and also showed significantly greater duration (PTD) scores for the JQ call than both naïve ($z = 2.31$, effect size = −.32, $p = .01$) and 8-min yoked, NOC ($z = 2.36$, effect size = .35, $p = .009$) chicks (see Fig. 2). These chicks failed, however, to show significantly shorter latency (PTTA difference) scores for the JQ call than naïve ($z = -.84$, effect size = .12, $p = .202$) and NOC ($z = -1.56$, effect size = −.23, $p = .06$) chicks. These chicks also showed no significant difference in either duration ($z = 1.04$, effect size = −.15, $p = .149$) or latency ($z = -.51$, effect size = .07, $p = .305$) scores from chicks given 5-min CON exposure to the JQ call.

Chicks given 10-min CON exposure to the JQ call, on the other hand, showed no preference for the JQ call, $\chi^2(2,\ N = 34) = 7.29$, $w = .46$, $p = .026$, and showed significantly longer duration ($z = -2.61$, effect size = .51, $p < .005$) but not shorter latency scores ($z = -.69$, effect size = .14, $p = .245$) for the BW over the JQ maternal call. These chicks showed duration ($z = 1.45$, effect size = −.20, $p = .073$) and latency ($z = -1.45$, effect size = .20, $p = .073$) scores for the JQ call that were not significantly different from scores of naïve subjects. These chicks also showed duration ($z = -1.34$, effect size = .20, $p = .09$) and latency ($z = 1.19$, effect size = −.17, $p = .118$) scores for the JQ call that were not significantly different from scores of yoked, NOC subjects. In addition, these chicks showed significantly *smaller* duration ($z = -1.87$, effect size = .11, $p = 0.31$) but not latency ($z = .48$, effect size = −.07, $p = .316$) scores for the JQ call than chicks given 5-min CON exposure to the JQ call.

Both chicks given 8-min yoked, NOC exposure, $\chi^2(2,\ N = 31) = 18.26$, $w = .77$, $p < .0005$, and chicks given 10-min NOC exposure, $\chi^2(2,\ N = 29) = 9.17$, $w = .56$, $p = .01$, showed a strong preference for the BW maternal call. Chicks given 8-min NOC exposure to the JQ call showed significantly larger duration ($z = -4.21$, effect size = .87, $p < .00005$) and shorter latency ($z = 3.8$, effect size = .78, $p < .0001$) scores for the BW over the JQ maternal call. Chicks given 10-min NOC exposure to the JQ call likewise showed significantly larger duration ($z = -2.8$, effect size = .59, $p < .002$) and shorter latency

($z = -1.74$, effect size = .37, $p = .02$) scores for the BW over the JQ maternal call.

As can be seen in Table 1, chicks given 8-min, $\chi^2(2, N = 32) = 18.1$, $w = .75$, $p < .0002$, and 10-min, $\chi^2(2, N = 31) = 23.48$, $w = .87$, $p < .00001$, CON exposure to the BW call all showed significant preferences for the BW call. Chicks given 8-min CON exposure also showed significantly larger duration ($z = -3.53$, effect size = .72, $p = .0002$) and shorter latency ($z = -1.66$, effect size = .34, $p < .05$) scores for the BW over the JQ call. Chicks given 10-min CON exposure likewise showed significantly larger duration ($z = -4.0$, effect size = .82, $p < .00005$) and shorter latency ($z = -3.12$, effect size = .64, $p < .001$) scores for the BW over the JQ call.

Between group comparisons revealed that chicks given 5-min ($z = 1.32$, effect size = −.18, $p = .185$) and 8-min ($z = .96$, effect size = −.13, $p = .335$) CON exposure to the BW call did not show a significant difference in duration (PTD) scores from naïve chicks (see Fig. 3). Chicks given 5-min ($z = .85$, effect size = −.12, $p = .397$) and 8-min ($z = -.40$, effect size = .06, $p = .344$) CON exposure also showed no difference in latency (PTTA difference) scores for the BW call from naïve chicks. Chicks given 10-min CON exposure, however, showed significantly greater duration ($z = 1.71$, effect size = −.24, $p = .043$) but not latency ($z = .71$, effect size = −.10, $p = .240$) scores for the BW call than naïve chicks.

Contrary to our predictions, our results reveal a pattern of decreasing preference for the JQ maternal call as the amount of contingent exposure to the call was increased. Chicks given 8-min CON exposure to the JQ call showed preferences for the JQ call similar to chicks given 5-min CON exposure. Chicks given 10-min CON exposure to the JQ call, on the other hand, showed preferences for the JQ call similar to those of both naïve and yoked, NOC subjects. This pattern of results suggests that BW chicks might respond to longer training sessions as increasingly aversive and thus come to experience the JQ call as aversive via association with this context. Our results with the BW maternal call, however, indicate a pattern of increasing levels of preference for the BW call with increased contingent exposure to that call. This provides evidence that chicks do not simply acquire an aversion to an auditory stimulus with increased amounts of contingent exposure. These results also suggest that chicks respond differentially to the length of a contingent training session depending on whether the training stimuli are of conspecific or heterospecific origin.

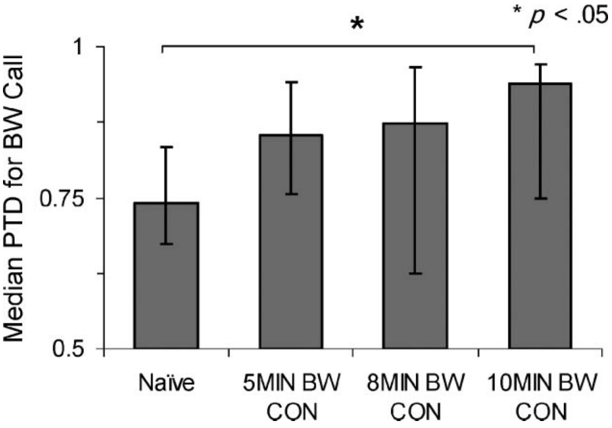

FIGURE 3 Median proportion of total duration (PTD) scores (±95% CI) for the bobwhite maternal call for naïve subjects and subjects exposed to the BW call in Experiments 1 and 2. Significance indicated is for Mann–Whitney *U* tests.

Given that variable interval and variable ratio (VR) schedules are known to produce higher and more steady rates of responding in operant paradigms than fixed interval and fixed ratio (FR) schedules (e.g., Catania, 1992), we were interested in whether the use of a variable rather than a FR schedule of stimulus presentation would facilitate the acquisition of species-atypical preferences for the heterospecific, JQ maternal call over and above the levels displayed by chicks provided with FR1 exposure to the JQ call in Experiment 1. We addressed this possibility in the next experiment.

EXPERIMENT 3: SCHEDULE OF CONTINGENCY AND THE MALLEABILITY OF AUDITORY PREFERENCES IN NORTHERN BOBWHITE NEONATES

The purpose of this experiment was to examine the effects of introducing variability to the schedule of contingent stimulus presentation on the acquisition of preferences for a heterospecific quail call in BW chicks. In Experiments 1 and 2 chicks received a single playback of the maternal call for each contact vocalization emitted during training. Given well established findings within the operant learning literature (e.g., Catania, 1992; Ferster & Skinner, 1957), we hypothesized that introducing variability to this schedule would have a greater effect on chick preferences for the JQ maternal call than the fixed 1:1 schedule employed in Experiments 1 and 2. Specifically, we predicted that chicks provided with variable ratio (VR2) exposure, in which they sometimes vocalize once, sometimes twice and sometimes three times to hear the JQ maternal call (hearing the call on average once every two times that they vocalize) would show a preference for that call over their conspecific BW maternal call in simultaneous choice tests between the two calls. We also predicted that chicks given such VR exposure to the JQ call would show significantly greater preferences for the JQ call than chicks provided with equivalent FR exposure.

Methods

Subjects. One hundred six maternally naïve, incubator reared BW chicks served as subjects. Chicks provided with contingent training were on either a fixed ($N = 37$) or variable ($N = 37$) ratio schedule were trained and tested first. Of these, three chicks failed to vocalize during FR2 training sessions and six during VR2 sessions and were excluded from the study. No chicks were yoked to FR2 chicks given the low levels of preference for the JQ call displayed by FR2 chicks. Chicks yoked to VR subjects ($N = 32$) were trained and tested after these.

Procedure. Chicks provided with CON exposure to the JQ call were provided with exposure to the call on either a variable ratio (VR2) or fixed ratio (FR2) training schedule. Chicks on the VR2 schedule received a single playback of the JQ call an average of once for every two contact vocalizations emitted ($M = 1.996$, SD $= .141$) during their training sessions. This was achieved via the computer program used to track chick vocalizations, which was programmed to randomly select a 1:1, 1:2, or 1:3 schedule initially and after each call playback (with no runs greater than 2) and to play the JQ call accordingly. Chicks in the FR2 condition were played the JQ call by a similar program on a FR of once for every two vocalizations emitted. Each subject in the NOC condition was yoked individually to a chick in the VR2 condition, as previously described. Yoked subjects were not obtained for the FR2 schedule because of the low levels of preference displayed by CON FR2 chicks (see below). All subjects were tested on Day 2 post-hatch in individual simultaneous choice tests between the JQ and BW maternal calls.

Results and Discussion

Training. Vocalization and playback data are displayed in Table 2. As would be expected, we found that chicks provided both with VR2 ($t = -2.56$, $p < .007$, power $= .81$) and FR2 ($t = -3.41$, $p < .0006$, power $= .96$) exposure to the JQ call vocalized more frequently during their training sessions than chicks provided with FR1 exposure in Experiment 1. Chicks given VR2 exposure also heard the call significantly fewer times than chicks given FR1 exposure ($t = 9.55$, $p < .000001$, power $= 1.0$), as did chicks given FR2 exposure ($t = 8.45$, $p < .000001$, power $= 1.0$).

Testing. As can be seen in Table 3, chicks provided with CON exposure to the JQ call on a VR2 schedule showed a significant preference for the JQ call, $\chi^2(2, N = 32) = 7.75$, $w = .49$, $p = .021$, whereas both chicks provided with yoked exposure, $\chi^2(2, N = 24) = 12.25$, $w = .71$, $p = .002$, and exposure on an FR2 schedule, $\chi^2(2, N = 31) = 13.6$, $w = .66$, $p = .001$, displayed significant preferences for the BW maternal call.

Chicks given CON VR2 exposure to the JQ call showed significantly larger duration ($z = -1.95$, effect size $= .39$, $p = .026$) but not shorter latency ($z = -1.38$, effect size $= .28$, $p = .083$) scores for the JQ than the BW maternal call (see Fig. 4). Chicks given yoked exposure to the JQ call, in contrast, showed significantly larger duration ($z = 1.8$, effect size $= .42$, $p = .036$) and shorter latency ($z = -1.8$, effect size $= .42$, $p = .036$) scores for the BW than the JQ call. Chicks given CON FR2 exposure to the JQ call likewise showed significantly larger duration ($z = -1.96$, effect size $= .40$, $p = .025$) and shorter latency

Table 2. Mean Number of Contact Vocalizations and Call Playbacks (and SDs) for Experiments 1–3

Condition	*n* Trained	# of Contact Voc.	# of Call Playbacks
Experiment 1			
JQ FR1 contingent (5 min)	38	34.8 (7.7)	34.8 (7.7)
JQ yoked (5 min)	38	30.2 (17.0)	34.8 (7.7)
BW FR1 contingent (5 min)	32	28.5 (6.4)	28.5 (6.4)
Experiment 2			
BW FR1 contingent (8 min)	36	43.9 (11.6)	43.9 (11.6)
BW FR1 contingent (10 min)	36	55.7 (13.5)	55.7 (13.5)
JQ FR1 contingent (8 min)	32	59.5 (9.9)	59.5 (9.9)
JQ FR1 yoked (8 min)	32	54.8 (25.2)	59.5 (9.9)
JQ FR1 contingent (10 min)	34	69.8 (15.9)	69.8 (15.9)
JQ FR1 yoked (10 min)	34	[a]	69.8 (15.9)
Experiment 3			
JQ VR2 contingent	32	39.4 (7.7)	21.4 (3.8)
JQ yoked (VR2)	32	39.5 (17.6)	21.4 (3.8)
JQ FR2 contingent	34	42.2 (10.6)	22.1 (4.9)

[a] These data were mistakenly not collected for these subjects.

Table 3. Preferences for the Japanese and Bobwhite Quail Maternal Calls in Experiment 3

		Preference		
Condition	*n* Responding	Japanese	Bobwhite	NP
JQ VR2 contingent	32	18*	8	6
JQ VR2 yoked	24	8	15**	1
JQ FR2 contingent	31	6	20**	5

*$p < .05$.
**$p < .005$.

($z = -2.76$, effect size = .57, $p < .003$) scores for the BW than the JQ call.

Between group comparisons revealed that chicks provided with CON VR2 exposure to the JQ call had duration scores for the JQ call that were significantly greater than scores of naïve ($z = 3.95$, effect size = −.54, $p < .00005$), yoked VR2 ($z = -2.38$, effect size = .37, $p < .009$) and FR2 ($z = 2.92$, effect size = −.41, $p < .002$) chicks and approached a significant difference from the scores of FR1 chicks in Experiment 1 ($z = 1.43$, effect size = −.20, $p = .076$; see Fig. 5). Chicks provided with VR2 exposure also showed latency scores for the JQ call that were significantly shorter than scores of naïve ($z = -2.8$, effect size = .39, $p = .005$), yoked VR2 ($z = 2.42$, effect size = −.38, $p < .008$), and FR2 ($z = 3.38$, effect size = −.50, $p < .0005$) but not FR1 chicks ($z = -1.0$, effect size = .14, $p = .16$). Chicks provided with yoked VR2 exposure to the JQ call showed no difference in duration ($z = -.53$, effect size = .08, $p = .597$) or latency ($z = .94$, effect size = −.14, $p = .346$) scores for the JQ call from naïve chicks. Chicks provided with FR2 exposure to the JQ call also showed no difference in duration ($z = -.8$, effect size = .11, $p = .425$) or latency ($z = 1.5$, effect size = −.21, $p = .135$) scores for the JQ call from naïve chicks.

These results indicate that a VR has a greater effect than a FR schedule of contingent stimulus presentation on the malleability of species-typical preferences in BW hatchlings. Chicks provided with contingent exposure to the JQ call on a VR2 schedule showed a significant preference for the JQ call, despite having heard the call significantly fewer times than chicks provided with FR1 exposure. Chicks provided with contingent exposure to the JQ call on an FR2 schedule, on the other hand, showed no difference in responding from naïve chicks, despite having heard the call the same number of times, on average, as VR2 chicks. Chicks yoked to VR2 chicks also showed no difference in their preferences from naïve chicks. These findings add support to the statement that the overall amount of exposure to a stimulus is frequently less important for learning and perceptual development than the nature (Harshaw & Lickliter, 2007; Lickliter, Bahrick, & Honeycutt, 2002) or timing (Columbus &

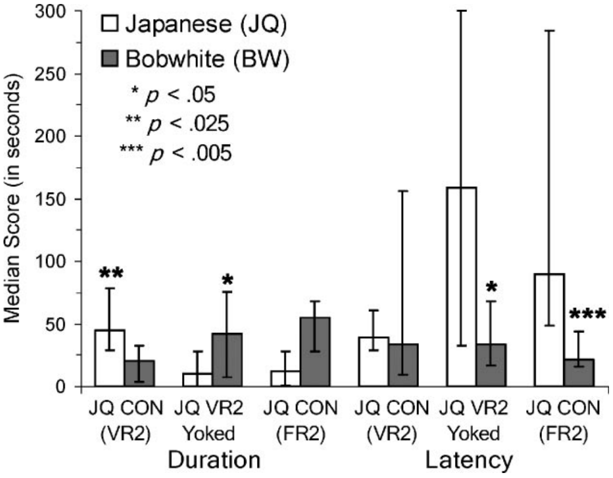

FIGURE 4 Median duration and latency scores (±95% CI) for the Japanese and bobwhite quail maternal calls for Experiment 3. Significance indicated is for Wilcoxon matched-pairs signed-ranks tests.

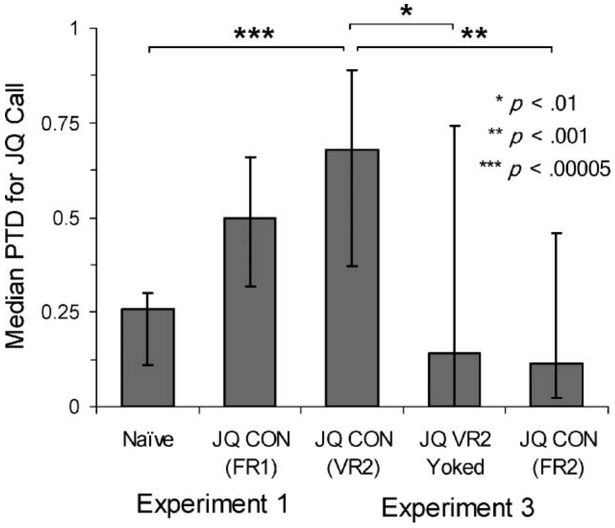

FIGURE 5 Median proportion of total duration (PTD) scores (±95% CI) for the Japanese quail call for Experiment 3. A PTD score of .5 indicates no preference for either call. Significance indicated is for Mann–Whitney *U* tests.

Lickliter, 1998; Honeycutt & Lickliter, 2001; Lickliter, 1993; Banker & Lickliter, 1993; Sleigh & Lickliter, 1998) of that exposure.

GENERAL DISCUSSION

The current study demonstrates that stimulus contingency can facilitate the malleability of species-typical auditory preferences in Northern BW hatchlings. We confirmed that BW chicks normally show strong species-typical preferences for their conspecific BW maternal call over the maternal calls of other species (e.g., Banker & Lickliter, 1993; Lickliter & Virkar, 1989). We also found that chicks provided with exposure to a JQ maternal call contingent upon their own contact vocalizations during a single 5-min session no longer displayed a preference for their conspecific maternal call. No such effect was observed in chicks given yoked, noncontingent exposure to the call. This finding replicates and extends the findings of Harshaw and Lickliter (2007), who found a significant difference in preferences for a familiar conspecific maternal call between chicks provided with brief contingent and chicks provided with brief noncontingent exposure to that call.

The current study also demonstrates that lengthening the amount of exposure to a vocal-auditory contingency is ineffective at further increasing BW chick preferences for a heterospecific call. Chicks provided with 8- or 10-min contingent training sessions showed a pattern of decreasing preference for the JQ call with increased exposure to the call. This was not likely due to the acquisition of an aversion to the call, as chicks provided with increased levels of exposure to the conspecific BW maternal call showed a pattern of increasing preference for that call with increased session length. Chicks provided with 10-min contingent exposure to the BW call moreover showed significantly greater preferences for that call than naïve chicks, whereas chicks provided with 10-min contingent exposure to the JQ call showed no differences from the scores of naïve chicks. This pattern of findings suggests that the conditions conducive to the acquisition of auditory preferences via stimulus contingency vary as a function of the species-specificity of the stimuli employed.

Why would more stimulation not produce better learning? Interestingly, Tchernichovski, Lints, Mitra, and Nottebohm (1999) obtained parallel results in a study of song imitation in young zebra finches. In their study, juvenile males were provided with access to a contingency between pecking at a key and the playback of an adult male song exemplar. These authors found a strong negative correlation between increased access to the contingency and the later quality of song imitation by these males. Males that were allowed *ad libitum* access to the contingency in fact showed the lowest quality of song imitation. These authors interpreted their findings as reflecting a process of ‘‘model overabundance’’ encouraging a ‘‘winnowing of song repertoire’’ and the fostering of individuality in male song. It seems more likely, however, that under many conditions young organisms will habituate to and/or lose interest in stimuli presented and/or encountered in a highly predictable manner (either *ad libitum* and/or on a fixed schedule) without more attractive, biologically and/or developmentally important ‘‘secondary’’ stimuli paired with or following these stimuli. In the current study, for example, chicks may have lost interest in the heterospecific call once the novelty of the contingency waned, given that the contingency did not provide anything more developmentally attractive/relevant to the chick (e.g., visual or physical contact with a hen, heat, and/or escape from the testing arena). Given that chicks already had a strong preference for the species-typical BW maternal call, the same pattern of influence would not be expected to hold for this call.

The present study also examined the effects of introducing variability to the schedule of contingent stimulus presentation on the acquisition of auditory preferences for a JQ maternal call by BW chicks. We found that providing chicks with a 5-min contingent exposure to the JQ call on a VR2 schedule (i.e., they heard the maternal call once for every two contact vocalizations emitted, on average) had a greater influence on chick preference for the JQ call than either FR1 or FR2 exposure. The use of a VR2 schedule moreover engendered a reversal of species-typical preferences or significant preference for the JQ over the BW maternal call in BW hatchlings. Chicks provided with either yoked exposure or contingent exposure on an FR2 schedule, in contrast, showed no difference in their auditory preferences from naïve chicks. This finding is particularly striking when contrasted with the fact that either 11–30 hr of exposure to a chicken maternal call and devocalization (Gottlieb, 1987, 1991a) or 11–30 hr of exposure and social/tactile rearing (Gottlieb, 1991b, 1993) were found to be required for mallard ducklings to show a reversal of their species-typical preferences for the mallard maternal call in favor of the chicken maternal call.

Why would a variable schedule of contingency engender greater preferences for a heterospecific quail call than a fixed schedule? The observation that variable schedules produces higher and more steady levels of responding than fixed schedules has been long established in the learning literature (e.g., Ferster & Skinner, 1957). It is also well established that given a choice between a variable and FR schedule, a variety of species will prefer the VR over the FR schedule (e.g., Fantino, 1967; Field, Tonneau, Ahearn, & Hineline, 1996; Rider, 1979; Sherman & Thomas, 1968), even when this schedule provides fewer reinforcers or less stimulation (e.g., Ahearn, Hineline, & David, 1992). Such a preference for variability implies an affective and/or motivational response to stimuli encountered or delivered with a higher degree of variability that could facilitate learning and memory. In support for such a view, it has been shown that unpredictable stimulation can selectively activate reward structures in the brain such as the nucleus accumbens, thalamus, and medial orbitofrontal cortex (Berns, McClure, Pagnoni, & Montague, 2001) and that the phasic firing of dopaminergic neurons is selective to unpredictable reward-signaling stimulation (Fiorillo, Tobler, & Schultz, 2003; Hollerman & Schultz, 1998; Schultz, 2002).

Watson (1972, 2001) and others have argued that degree of stimulus contingency can be seen as providing an invariant ground for the early discrimination both of ‘‘self’’ from ‘‘other’’ (e.g., Bahrick & Watson, 1985; Miyazaki & Hiraki, 2006; Rochat & Morgan, 1995; Schmuckler & Jewell, 2007) and of social from nonsocial stimulation in general (e.g., Gergely & Watson, 1999; Watson, 1972). In this view, a high degree of contingency (or ‘‘perfect contingency’’) invariantly stems from self-initiated action, particularly from the manipulation of one’s own body and nonsocial objects. Lesser degrees of contingency, on the other hand, are seen to be a consequence and/or correlate of interaction with a social partner. From this perspective, highly predictable stimulation may be experienced as less social or even nonsocial compared to stimulation that has a more unpredictable (or ‘‘imperfect’’) relation to the organism’s activity. It is thus possible that chicks provided with VR2 exposure to the heterospecific call perceived this exposure as more social (or at least more attractive, arousing, and/or interesting) than equivalent FR exposure.

The observation that the species-specific preferences of precocial birds are malleable is obviously not novel, dating back to Douglas Spalding (1873), and being the source of the term ‘‘imprinting.’’ Over the course of the 20th century, the study of filial imprinting was undertaken largely as if it were both a nonsocial process (cf. Lickliter & Gottlieb, 1985; Lickliter et al., 1993) and a special type of learning, occurring independent of reinforcement or contingency (e.g., Lorenz, 1937). However, the developmental ecology of most precocial birds contains regular opportunity for social interaction with adults and broodmates beginning very early in development (e.g., Tuculescu & Griswold, 1983; Vince, 1972). A key feature of such interaction is undoubtedly the experience of social contingencies. We previously demonstrated that stimulus contingency can have a significant effect on the early acquisition of auditory preferences in precocial quail chicks (Harshaw & Lickliter, 2007). The current study shows that contingent stimulation, particularly when delivered on a variable schedule, is also capable of engendering a high degree of malleability in the species-specific auditory preferences of precocial quail chicks. Such malleability could be seen as ‘‘maladaptive’’ were it not for the fact that a normally occurring feature of the rearing environment for most precocial birds is the presence of an incubating hen and broodmates of the appropriate species. These conspecifics provide a rich source of social stimulation that appears to effectively narrow the young hatchling’s range of responsiveness to species-atypical stimulation. Our findings suggest that modifying the nature or availability of this species-typical social stimulation can lead to enhanced malleability of auditory preferences, at least during early postnatal development.

NOTES

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