Birdsong is considered a model of human speech development at behavioral and neural levels. Few direct tests of the proposed analogs exist, however. Here we test a mechanism of phonological development in human infants that is based on social shaping, a selective learning process first documented in songbirds. By manipulating mothers’ reactions to their 8-month-old infants’ vocalizations, we demonstrate that phonological features of babbling are sensitive to nonimitative social stimulation. Contingent, but not noncontingent, maternal behavior facilitates more complex and mature vocal behavior. Changes in vocalizations persist after the manipulation. The data show that human infants use social feedback, facilitating immediate transitions in vocal behavior. Social interaction creates rapid shifts to developmentally more advanced sounds. These transitions mirror the normal development of speech, supporting the predictions of the avian social shaping model. These data provide strong support for a parallel in function between vocal precursors of songbirds and infants. Because imitation is usually considered the mechanism for vocal learning in both taxa, the findings introduce social shaping as a general process underlying the development of speech and song.

Birdsong is often considered a model for speech development in humans (1–4). The early vocalizations of both taxa are immature and unstable when compared with adult forms. In addition, the vocalizations of both birds and babies develop by a combination of selective attrition and learning of novel forms. Young songbirds initially produce subsong, characterized by high variability in structure and timing (5). The acoustic and motor patterns of subsong are qualitatively distinct from those of adult forms. It is sung at low amplitude and includes elements that will not be present in adult song. This early phase is followed by a period of plastic song, which contains notes and whistles characteristic of adult song, but these elements are poorly articulated and are not sung in a stable order. During plastic song, some elements are repeated and retained whereas others are dropped from the repertoire. Over time, plastic song gradually reduces into crystallized song, comprising a limited set of species-typical song features.

The structural and temporal variations of subsong and plastic song are similar to those found in the precanonical and canonical babbling of human infants. Infraphonology (6) describes changes in prelinguistic vocalizations as they gradually become more speech-like during the first year (Fig. 1). From birth to approximately 7 months, vocal development proceeds from the earliest quasi-resonant sounds by the addition of new forms of vocal behavior, such as fully resonant vowels and marginal syllables. Further development, however, is characterized by a loss of acoustic variability as vocal behavior stabilizes on canonical forms: the sound types and patterns of the native language.

Are cross-taxa parallels in early vocal behavior accompanied by similarities in mechanisms of development? Previous comparisons (1, 3) focused on maturation of motor and memory abilities and concluded that vocal development in both taxa was driven by imitation and constrained by maturation of the articulators. These findings reflected the traditional perspective on human vocal development, in which maturation of the articularators drives the development of learning to talk (7–11). However, the maturational perspective incorporates several assumptions: that only internal causes are important, that infants play a passive role in development, and that the prelinguistic vocalizations that characterize the first year are merely the disorganized output of an immature system, having no functional significance for vocal development.

Songbird vocal development is sensitive to the responses of conspecifics (2, 12–15). Two forms of social influence have been found. In action-based learning, social interaction in the form of countersinging exchanges between adult and young facilitates the retention of already existing components of plastic song (2, 15). In social shaping, selective reinforcement of vocal precursors by social companions biases learning toward certain vocal forms and facilitates the development of crystallized song (12–14). Is vocal development in humans similarly influenced by the actions of social partners? Although both types of learning have been proposed as potential models of human vocal development (2, 16), few direct tests have been conducted of proposed analogs in mechanisms of development between birdsong and speech. The objective of the current study was to determine the relationship between social feedback and vocal development by assessing the sensitivity of early vocalizing to the behavior of caregivers. Does social contingency provide opportunities for vocal learning? Can infants learn from caregivers’ reactions to their sounds? It is known that the vocal behavior of infants is responsive to contingent reinforcement. Studies of contingent versus noncontingent social reinforcement have documented the effects of receiver responses on vocal production. Contingent responses from adults such as touching, smiling, and shaking a rattle are effective reinforcers of infant vocalizations, leading to increased rates of production (17–20). These findings provide evidence that the responses of social partners can influence infants’ vocal behavior. However, these learning studies aimed to modify only the frequency of vocalization and did not differentiate among types of sounds, so the influence of contingent responding on changes in vocal quality was not examined. In addition, the interactions between infants and experimenters were highly constrained, because infants were placed in cribs or chairs with little else to do except attend to the persons sitting or standing in front of them. The relationship between social interaction and developmental transitions has rarely been studied, although the amount of mutual engagement between 2- to 6-month-old infants and social partners has been shown to be related to the number of speech-like vocalizations produced (21, 22).

We tested infants’ ability to use social feedback to facilitate developmental transitions in vocal behavior. We studied 8-month-old infants because their vocal behavior is in transition between the rudimentary sounds that characterize the first months of life and the stable canonical syllables that emerge by the end of the first year (Fig. 1). The acoustic variability inherent

Abbreviations: CC, contingent condition; YC, yoked-control condition.

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in the transitory state allows for examinations of the sensitivity of the system to social perturbations.

Methods

Participants. Thirty infants (mean age, 8 months 14 days; range, 6 months 29 days to 10 months 22 days) and their mothers participated in the study. Participants were recruited from birth announcements in the local newspaper. Infants were first assigned to the experimental (contingent) condition (CC; n = 15; mean age, 8 months 7 days); the yoked-control condition (YC; n = 15; mean age, 8 months 21 days) was run after the completion of the experimental condition. The data from an additional nine infants could not be used in the study; five infants became upset during the procedure, and four parents could not be scheduled for the second (test) session. We attempted to schedule the two sessions 24 h apart. Eight infants had the second session later in the same day, 19 had the second session 24 h later, and 3 had the second session 48 h later.

Apparatus. The study took place in a 4.5 × 3.2 m playroom containing toys and picture boards. The large size of the playroom allowed infants to locomote and explore so that they were not forced into proximal interactions with their mothers. Behavior was recorded by using three wall-mounted cameras (Handycam TR-100, Sony, Tokyo), routed to an SVHS video tape recorder (AG1980, Panasonic, Secaucus, NJ) by a video mixer (Videonics MX-1, Focus Enhancements, Campbell, CA) that allowed selection of the best camera angle. Input from the infant’s wireless microphone (FMR-150, Telex Communications, Burnsville, MN) was routed to the left stereo channel of the video tape recorder by an audio mixer (1604 VLZ, Mackie Designs, Woodinville, WA). The experimenter’s instructions were recorded by a head-worn microphone (PRO8HE, Audio-Technica, Stow, OH) and routed by the mixer to both the mother’s wireless headphones (Optimus 33–1165, Radio Shack, Ft. Worth, TX) and to the right stereo channel of the video tape recorder.

Procedure. To study the influence of social interaction on vocalizing, we observed mothers and their infants as they engaged in two 30-min play sessions (Fig. 2). The first session served to familiarize the mothers and infants with the playroom setting. In the second session, we manipulated the contingency between mothers’ responsiveness and infants’ vocal production. Mother–infant dyads first engaged in a 10-min “baseline” period of unstructured play to establish initial levels of infant vocalizations and maternal responses. To investigate the role of contingency in vocal learning, the timing of mothers’ responding was then manipulated. During a second 10-min “social response” period, mothers were asked to respond by smiling and moving closer to and touching their infants (Fig. 3). Half of the mothers (CC) were told to react immediately after their infants vocalized, and half (YC) were instructed to respond by the experimenter on the basis of the response schedules generated by the CC mothers. Pairings between CC and YC mothers were random. YC mothers’ responses were thus linked to those of the CC mothers so that the control infants received the same amount of social

Fig. 1. We measured four infraphonological parameters of prelinguistic vocalizations. A quasi-voiced sound (a) is produced by a partially closed vocal tract and has a high degree of nasality and creaky voice. In contrast, a fully voiced vowel (b) is produced with an open vocal tract and has full resonance and a clear formant structure. A marginal syllable (c) consists of a slow sequence of consonant–vowel (CV) articulation with a long CV transition. In contrast, a canonical syllable (d) meets the acoustic criteria for well formed speech, with a total length of 50–500 ms and a rapid CV transition of 25–150 ms.
stimulation (an identical number of responses) as those in the CC, but the stimulation was not synchronized with their vocal behavior.

During the last 10-min “extinction” period, mothers and infants again engaged in play, with no instructions as to the nature of their responsiveness, thus extinguishing the contingencies of responsiveness that had been induced in the previous period. The extinction period also controlled for the potential confound of infants’ tendency to increase their rate of vocalizing as they become familiar with the testing environment. Participants did not know that vocal behavior was the focus of the study. The mothers were told that infant play was the behavior of interest.

During all three periods, we measured the number of vocalizations to which mothers responded, the total number of infant vocalizations, and several infraphonological parameters of the infants’ sounds. The number of vocalizations that mothers responded to was calculated by counting each sound that received a response within one second after cessation. All vocalization coding was done by the first author and an additional observer trained in the infraphonological system. Both observers coded all of the infants. Average interobserver reliability for each group was 0.90 (range, 0.81–0.96). We analyzed the maternal response and vocalization data by using Friedman ANOVA-by-ranks tests and, where appropriate, post hoc tests on group differences (23).

Results

CC infants significantly increased the number and quality of vocalizations in the social response period. Their sounds were phonologically more advanced than the sounds they produced during baseline. YC infants vocalized frequently but showed no change in the developmental quality of their babbling. Both groups’ overall pattern of vocalizing differed across conditions. CC infants’ total number of vocalizations tracked their mothers’ level of contingent responsiveness (Fig. 4). A significant effect of test period on the proportion of syllables to total vocalizations (Fr = 9.73, P < 0.01) was found for both CC and YC infants. CC infants produced more sounds during social response (P < 0.05) than baseline. In contrast, YC infants did not show changes in their rate of syllable production (Fr = 0.79, not significant). Of the syllables produced, only the CC infants increased their rate of syllable production during social response (P < 0.05) than baseline. Infants in the CC and eight in the YC group produced canonical syllables. A significant effect of test period on the proportion of canonical syllables to total syllables was found for CC infants from baseline to the social response period, because the amount of chance contingency during social response was equal to the level of maternal responsiveness in baseline and extinction periods (Fig. 4). YC infants produced more sounds during extinction than in baseline (P < 0.05). This rise was likely due to an increase in social behavior by the YC mothers after the change in response schedules.

CC infants changed several infraphonological features of their sounds in ways that were not observed in the YC infants. CC infants increased their rate of syllable production in the social response period (Fig. 5), yielding a significant effect of test period on the proportion of syllables to total vocalizations (Fr = 9.73, P < 0.01). CC infants produced more syllables during social response (P < 0.05) than baseline. In contrast, YC infants did not show changes in their rate of syllable production (Fr = 0.79, not significant). Of the syllables produced, only the CC infants increased their output of canonical syllables from baseline to extinction (Fig. 5). Not all infants produced canonical syllables, reducing the number of cases available for analysis. Ten infants in the CC and eight in the YC group produced canonical syllables. A significant effect of test period on the proportion of canonical syllables to total syllables was found for CC infants.
CC infants produced more syllables during extinction ($P < 0.05$) than baseline. In contrast, YC infants did not change the form of their syllables ($Fr = 2.60$, not significant).

CC infants’ sounds were more fully voiced in the social response period (Fig. 5), yielding a significant effect of test period on the proportion of fully voiced vocalizations to total number of vocalizations produced ($Fr = 21.73, P < 0.0001$). CC infants produced more fully voiced sounds during social response ($P < 0.05$) and extinction ($P < 0.05$) than baseline. Their sounds retained a high proportion of full voicing during the extinction period, even though their rate of vocalizing in extinction had decreased to baseline levels (Fig. 5). YC infants, however, did not show a change in voicing ($Fr = 0.93$, not significant).

**Discussion**

Contingent social interactions increased the proportions of vocalizations that had more mature voicing, syllable structure, and faster (canonical) consonant–vowel transitions. Compared with the high proportions of quasi-voiced sounds, simple vowels,
and marginal syllables that characterized CC infants’ baseline vocalizations, the observed changes in sound production were in a developmentally advanced direction. Contingent interactions thus facilitated changes in vocal behavior that mirror developmental changes.

These data show that infants’ early vocal behavior is sensitive to perturbations of the social environment. In the large playroom where the study took place, infants were free to leave their mothers and explore the room, play with toys, or engage their caregivers by using nonvocal behavior. Even with much of the freedom they would have naturally, the infants’ sounds were tightly linked to the behavior of their caregivers.

What mechanisms mediate the observed relationship between increased contingency of social responsiveness and changes in the quality of vocal behavior? Previous work in our laboratory has shown that maternal behavior is sensitive to the infraphonological qualities of early sounds (e.g., voicing, syllable articulation) (24). Mothers showed more social responsiveness to babbling that contained more fully voiced and canonical sounds. Moreover, mothers showed this effect to unfamiliar infants, suggesting that early sounds have shared communicative content. Other work has shown that fully voiced prelinguistic vocalizations are more likely to be perceived by adults as communicative, increasing the probability of further adult responding (25). Thus, babbling both regulates and is regulated by social interaction. Such a system of reciprocal influences constitutes a social mechanism of vocal learning and development.

The idea that contingency perception can both reinforce and induce new forms of behavior stands in contrast to the current paradigm of human social learning. The current view relies on imitation, the copying of others’ behavior, as a mechanism of socially mediated developmental change (4, 26–29). Although studies show that behaviors taken to be evidence of imitative learning are really the products of more general processes like arousal (30, 31), little current research on social development seems to emphasize nonimitative learning (see reviews in refs. 32 and 33). As this study demonstrated, infants’ babbling changed in a lawful way without mothers providing behaviors that could serve as the basis for vocal imitation; they responded to infant sounds by smiling, moving closer to, and touching their infants. In addition, delayed imitation of adult mouth movements could not create the observed changes in voicing and consonant–vowel timing. The motoric foundations of early phonological development (e.g., increasing breath support, opening the back of the vocal tract, and producing faster tongue movements) are not directly observable by infants. Changes in babbling were not a result of maternal support, opening the back of the vocal tract, and producing syllables that characterized CC infants’ baseline vocalizations.

These data contain striking parallels to social mechanisms of vocal learning in several species of songbirds. In brown-headed cowbirds (Molothrus ater), young males produce variation in immature songs. Adult females use social gestures and displays that modulate the rate, quality, and retention of specific vocal patterns (34). Because female cowbirds do not sing, the mechanism at work cannot be imitation, the process often assumed to underlie song learning. Like human infants, sounds receiving social attention are more likely to recur. Contingency of social reinforcement is key; female cowbirds that display more social signals stimulate males to develop mature, more effective songs at a faster rate than those of males housed with females that allow less social interaction (35). In both taxa, vocal precursors have functional significance as part of a system of reciprocal influences between a young learner with a variable repertoire and a social environment that affects structured feedback.

Parallels in human and avian vocal development extend beyond cowbirds, because male white-crowned sparrows (Zonotrichia leucophrys) develop mature song types through action-based learning (2), which stems from acoustic feedback given by an adult male tutor that matches one of the pupil’s previously memorized song types. This form of contingency learning is evidenced by young males narrowing their repertoires when exposed to vocal tutoring in late spring. Thus, the young birds require interaction from the adults to develop crystallized song. As with the human infant data reported here, the important effect of conspecific responsiveness is not on the amount of vocalizing but on the articulatory quality of sounds produced and retained, as well as the immediacy of changes in vocal behavior.

These data are also relevant to understanding the neurobiology of avian song and human speech. Because social stimulation (with no auditory component) is shown here to influence the development of speech, neural structures must be involved in the speech system that are sensitive to nonauditory feedback. In songbirds, the song control region in the forebrain is well described but has been mapped from an auditory perspective (36). We know, however, that female cowbirds (which do not sing) show volumetric differences in the lateral magnocellular nucleus of the anterior neostriatum (IMAN) in relation to song responsiveness (37, 38), and that male cowbirds’ development of song is correlated with volume of a thalamic nucleus, Rt, in the visual system (39). The volume of Rt is larger in young males housed with females from local versus distant populations (39), indicating social influences on neural levels of organization. In addition, zebra finches (Taeniopygia guttata) show differential gene expression related to the social context of singing (40). Thus, the present work on social shaping suggests new areas for neurobiological study.

Our view is that early vocalizations become a channel of communication only after young birds or babies come to realize the instrumental value of sounds. The parallels in vocal development between birds and babies are in the synergy between adult responsiveness and the capacities of young organisms to use social information to refine their repertoires. In both taxa, what has been taken to be the disorganized output of an immature system has functional significance for later communicative development. If learning from cues in the social environment is important for early vocal development, then it should also be important for other parameters of word learning and language use. Current research on the acquisition of words (41) and grammar (42) shows that infants are capable of learning from environmental regularities. What is the role of statistical regularities in the social environment for language learning? Infants can perceive regularities in the behavior of others, in that they can parse a continuous stream of action into segments that tend to correspond with others’ intentions and thus have high predictive value for the infant (43). If babbling changes adults’ behavior in predictable, infant-oriented ways, then infants should be able to recognize changes in others’ actions as a result of their vocalizing. We believe that a more complete understanding of vocal ontogeny will emerge from the integration of social contingency perception with the timing and nature of conspecifics’ responsiveness to vocal precursors. These findings demonstrate the value of the avian model but suggest that we must look beyond the babble to find the performance-based processes responsible for vocal ontogeny.

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