Roles of Syntax Information in Directing Song Development in White-Crowned Sparrows (Zonotrichia leucophrys)

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Syntactical cues play an important role in song learning in songbirds. White-crowned sparrows (*Zonotrichia leucophrys*), whose song typically consists of four to five different phrases, fail to construct normal songs if exposed to all phrase types presented singly (Plamondon, Goller, & Rose, 2008; Soha & Marler 2001b). The specific role of acquired syntax information in guiding ontogenetic trajectories of syntax, however, and the respective contributions of instructive and selective processes to syntax ontogeny remain unknown. We tutored white-crowned sparrows with syntax information ranging from acoustic isolation to full song. Manipulation of tutor syntax influenced developmental trajectories of syntax assembly, suggesting that instructive processes contribute to syntax ontogeny. Early in development, birds tutored with full song or phrase pairs preferentially produced phrase pairings matching tutor syntax. Birds tutored with single phrases showed decreased diversity of pairwise syntactical combinations immediately after tutoring compared with other tutor groups, further illustrating the role of instructive processes. Overproduction of song material was also observed, suggesting that selective forces play a role in syntax development as well. Finally, consistent with the notion that innate influences guide syntax ontogeny, birds from all groups exhibited many similarities in trajectories of syntax assembly.

Keywords: white-crowned sparrow, Zonotrichia leucophrys oriantha, birdsong, vocal learning, song development

Oscine passerines must hear and memorize conspecific song during a sensitive period early in life to produce species-typical song (Konishi, 1965, 1985; Marler, 1970; Nelson, 1998; Thorpe, 1961). Songbirds may acquire specific song elements from tutors, as well as information regarding the temporal patterning or syntactic structure of song (in songbirds, *syntax* refers to the ordering of syllables and phrases). The song is gradually refined through a process of sensorimotor learning, which requires auditory feedback (Brainard & Doupe, 2002; Konishi, 1978; Solis, Brainard, Hessler, & Doupe, 2000). Different species of songbirds exhibit a wide range of syntactical and acoustic structure in their songs, from the single song of the chipping sparrow, which consists of a single note type, to the extensive repertoire of the nightingale, which consists of up to 200 syntactically complex song types.

Current studies continue to elucidate the ways in which acquired (tutor) information is used to guide song learning. Results of developmental studies can be viewed in the context of "selective" or "instructive" models of song learning. In a purely selective model of song learning, birds produce a variety of song elements that are innately specified and, via differential reinforcement, selectively maintain those that most closely match tutor models (Bottjer & Troyer, 2001; Margoliash, 2002; Marler, 1997). Alternatively, an instructive model of song learning posits that acquired tutor information directly guides song development and results in the expression of song features beyond those that are innately specified (Bottjer & Troyer, 2001). The duration of the developmental period, the volume of mate-

rial produced by birds, and technical limitations of analysis have constrained attempts to identify the roles of instructive, selective, and innate processes in song development. Nevertheless, many general features of song development have been elucidated. Marler and Peters (1982) described seven developmental stages in swamp sparrows. Three of the most easily discerned of these stages (subsong, plastic song, and crystallized song) have been widely observed in other oscine species and are thus thought to reflect a general pattern of vocal development in songbirds (Armstrong, 1963; Geberzahn & Hultsch, 2004; Kroodsma, 1974; Lanyon, 1960; Lemon & Scott, 1966; Marler & Peters, 1982; Poulsen, 1959). The subsong stage is characterized by soft, undeveloped vocalizations and is followed by a plastic song stage, during which recognizable precursors of tutor phrases emerge. Syntax (phrase or syllable order) during the plastic song stage is variable, and phonology (phrase or syllable morphology) remains unrefined. Marler and Peters (1982) noted a marked decrease in variability of song parameters as birds transitioned from plastic song to crystallized song; they also observed the phenomenon of overproduction, in

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which birds produced more syllable types during development than were included in their final songs.

Overproduction has been observed in several other species as well (Baptista, 1975; Marler & Peters, 1981; Nelson, 1992). Wild white-crowned sparrows ultimately crystallize a single song type, but they may produce a number of song types before eliminating those that do not closely match those of their territorial neighbors (Baptista, 1975, 1977; Baptista & King, 1980; Nelson, 2000). Nelson and Marler (1994) demonstrated in lab-reared white-crowned sparrows that song matching occurs via a process of overproduction and selective attrition rather than via the acquisition of novel songs late in development. This observation of action-based learning is an example of a selective process in song learning (Marler, 1997).

Although selective processes appear to play a role in song learning, there is evidence that tutor information may also directly guide, or instruct, learning trajectories. An instructive model of song learning predicts the emergence of song features beyond those that are innately specified as a result of exposure to tutor information (Bottjer & Troyer, 2001). Strong support for the contribution of instructive processes to song learning comes from the finding that several species of songbirds, including emberizid species, will learn heterospecific songs under certain conditions in the laboratory (e.g., Baptista & Petrinovich, 1986; Lanyon, 1960) and occasionally in the wild (Baptista, 1972, 1988; Baptista, Morton, & Pereyra, 1981; Eberhardt & Baptista, 1977). Tchernichovski, Lints, Mitra, and Nottebohm (2001) offered further support for instructive models of song learning with their finding that zebra finches under a delayed tutoring regime exhibited an abrupt increase in song feature diversity after exposure to tutor models. Song elements also became more structured at this time, suggesting that tutor information induced singing behaviors not previously exhibited.

Little is known about the respective roles of selective and instructive processes in the development of the syntactical organization of song, that is, the temporal arrangement of syllables and phrases. One possibility is that the progression from producing single phrases early in development to combinations of phrases later in development may largely be innately specified. Selective processes may then operate to eventually eliminate inappropriate combinations. However, syntactical information in tutor models may also play an early instructive role in the development of song syntax (Plamondon et al., 2008; Rose et al., 2004). This instructive process could influence the ordinal progression of syntax and direct the early establishment of particular syntactical combinations of syllables and phrases. Innate predispositions may also be involved in selectively guiding memorization of a species-typical model, whose implementation may then be guided by instructive processes.

Although several studies have focused on the effects of early syntax information on crystallized songs, relatively few studies have addressed how this information may influence song ontogeny. One such study examined the ontogeny of song syntax in the nightingale, whose song represents a high level of syntactical organization (Hultsch & Todt, 1989, 1992). Singing episodes in adults consist of multiple song types sung in a sequence labeled a *string*. Hultsch, Mundry, and Todt (1999) found that a syntactical hierarchy is established during song learning: Individual song types are acquired in a series and stored as packages, and packages are assembled into context groups, consisting of imitated songs garnered from the same tutor string in sequential order. However, potential instructive and selective roles of tutor syntax information in trajectories of syntax development in species whose syntax represents a lower level of complexity remain obscure. To more fully examine these roles, we tutored white-crowned sparrows with a variety of syntax models. We studied song ontogeny in birds raised in acoustic isolation and in birds tutored with varying levels of syntax information to determine the elements of syntax ontogeny that are guided by species-specific learning rules and those that may be guided by tutor information in an instructive or selective manner. A comprehensive study of song ontogeny can also offer insights into the development of learned communication behaviors in general. Song learning shares strong parallels with human speech learning (Doupe & Kuhl, 1999, 2008). The specific role of acquired information in directing human speech ontogeny during babbling is debated (e.g., Johnson, 1997; MacNeilage, Davis, Kinney, & Matyear, 2000). It is therefore interesting to explore whether this research can shed light on more general aspects of learned vocal behavior, including the ontogeny of speech.

Method

Collection

A detailed description of the collection and tutoring methods used in this experiment is provided in Plamondon et al. (2008). We collected 55 white-crowned sparrow nestlings (Zonotrichia leucophrys oriantha) ages 5-9 days over the years 2002-2005 from the Wasatch Mountain Range, Wasatch County, Utah. We hand-reared birds to independence and group-housed fledglings with 2-4 birds per cage. We began tutoring birds at 10-14 days of age and, at the onset of subsong (approximately 25 days of age), transferred birds exhibiting subsong (presumptive males; 44 birds total) to individual sound-attenuating chambers. Sound-attenuating chambers consisted of 12-in. \times 12-in. \times 16-in. Igloo Sportsman 100 coolers lined with sound-attenuating foam and provided an attenuation of approximately 30 dB for sounds in the range of 2-8 kHz. Birds in sound-attenuating chambers were kept on the natural photoperiod of the Wasatch Mountain Range for the duration of the study. Tutoring continued in the sound-attenuating chambers for a total (including preisolation tutoring) of 60 days.

Tutoring

We tutored birds with one of six tutoring regimes. Birds from five of these tutor groups (excluding the acoustic isolation group) were included in a previous study in which we reported that birds tutored with full songs produced crystallized songs that differed syntactically from those of birds tutored with phrase pairs or single phrases (see Plamondon et al., 2008, for spectrograms of tutor songs). The sixth group of birds received no tutoring (isolates). We recorded the crystallized songs of 2 adult male white-crowned sparrows from the same population and digitized songs (sampling rate = 25 kHz) using Signal (Engineering Design, Berkeley, California) or SASLab Pro (Avisoft, Berlin, Germany) sound AQ: 2 analysis software. These songs each consisted of five phrases: a whistle (A); a note complex (B); a high-pitched buzz (C); a second, lower-pitched buzz (D); and a second, distinct note complex (E).

Using SASLab Pro, we separated songs into individual phrases and constructed tutor songs for each tutoring group.

The six tutoring regimes consisted of full, wild-type song (Group 1); full song with phrases presented in reverse order (Group 2); normal (forward)-sequence phrase pairs (Group 3); reverse-phrase pairs (Group 4); phrases presented singly (Group 5); and no tutoring (acoustic isolation; Group 6). For Groups 3, 4, and 5, a silent interval of 2.5 s followed each phrase (Group 5) or phrase pair (Groups 3 and 4). For all groups, each full presentation of song (five single phrases for Group 5, four phrase pairs for Groups 3 and 4, and one presentation of full song for Groups 1 and 2) was followed by a silent interval of 13.5 s. We randomly selected the starting phrase or phrase pair for each session in these groups, but the order of presentation was always backward, that is, E, D, C, B, A for Group 5; DE, CD, BC, AB for Group 3; and BA, CB, DC, ED for Group 4, which should assemble an EDCBA song. We selected this bias in presentation order to ensure that birds could not use short-term memory to deduce the appropriate order from the incorrectly spaced but otherwise correct sequence of phrases. In each tutoring session, we broadcast the stimuli (about 78 dB SPL at the outer edge of the cage) for 10 min, with 1 min of silence separating each 10-min segment. We presented two 90-min tutoring sessions daily at 9:00 a.m. and 4:00 p.m. Two sets of tutor files were constructed using SASLab, each from the song of a single white-crowned sparrow. Each tutor song contained the same phrase order, but there were differences in the structure of individual phrases between songs (the note complexes differed in note composition, whereas the whistle and buzzes differed in pitch, direction, and timing of frequency and amplitude modulation; see Plamondon et al., 2008) that allowed us to distinguish between phrases copied from Tutor 1 and those copied from Tutor 2. These variants represent two song variants to which a whitecrowned sparrow nesting in the local segment of the Wasatch Mountain Range would be exposed. Because comparisons are made across groups and song variants do not represent classes of songs that we hypothesize will lead to differences in learning, pseudoreplication should not pose a problem to our statistical design (Kroodsma, Byers, Goodale, Johnson, & Liu, 2001). We used a die to randomly select the tutor (Tutor 1 or Tutor 2) that was heard in a given session; song from only one tutor was presented in any session. Digitized tutor files were broadcast from a PC using Windows Media Player software (Microsoft Corporation) and a Radio Shack M PA-45 35 W P. A. amplifier to individual speakers installed in each chamber (Projects Unlimited Inc. AT-261, Dayton, Ohio). Group 3 was tutored in 2002, Group 4 was split over the years 2002–2003, Group 5 was tutored in 2003, and Groups 1 and 2 were tutored in 2004. Group 6 (isolate group) was raised in 2005. Groups that were tutored in the same year were tutored in separate nonadjacent rooms to eliminate the possibility of exposure to inappropriate tutor information. Birds tutored with forwardorder phrase pairs constituted our first treatment group, at which time the sound-triggered recording set-up was still being refined, and we have only minimal acoustic data (insufficient to include in the analysis) from this group of birds during their first 120 days after tutoring. At the termination of each experiment, we sexed birds using either microsatellite DNA analysis (Griffiths, Double, Orr, & Dawson, 1998) or autopsy. The number of confirmed males for each group were 9, full forward; 8, full reverse; 7, forward pair;

5, reverse pair; 9, single phrase; and 6, isolates. After each experiment, birds were group-housed in university facilities.

Recording and Analysis

Immediately after the 60 days of tutoring, we began recording vocalizations using small condenser microphones (Radio Shack 33–3013) located in each sound-attenuating chamber, an Aardvark Pro Q10 eight-channel amplifier and sound card, and sound-triggered recording software (Avisoft). Throughout this study, all developmental time points are given with respect to the last day of tutoring. In the case of isolate birds, which were not tutored, developmental time points represent days elapsed from September 15 of the year of capture. We chose this date because it was the approximate end date of tutoring for birds from groups that received tutoring. Birds were tutored beginning at 10–14 days of age; the approximate age of a bird at any time point can thus be calculated by adding 70 days to the posttutoring day value. We continued recording until birds reached crystallization approximately 9 months later (June–July of the year after tutoring).

For each bird, we analyzed approximately 45 min of singing every 3-7 days. For a given day, we selected both long and short files that included singing at a variety of times during the day. A sound-triggered song file was terminated when a bird was silent for more than 1 min. For ease of storage and analysis, the maximum length of a given song file was set at 30 min. Identification of phrase types was performed chiefly by visual inspection (by Stephanie L. Plamondon and others). Scored data were subjected to spot checks by a second judge; for those data scored by a second judge (approximately 60% of the data included in our analysis), we included only phrases agreed on by both judges in our analysis. The remaining 40% of data that were not scored by a second judge consisted mainly of easily identifiable crystallized or nearcrystallized phrases. We used custom song recognition software written in MATLab to perform spot checks of some (approximately 10%) of these remaining data. For analyses of song from mid- to late plastic-song stages, we found a 97% correspondence between data sets derived from automated versus manual labeling methods. Differences between manual and automated results were largely attributed to differences in the scoring of occasional, ambiguous "hybrid" phrase types, which consisted of structural components of two types of syllables. We used additional software written in MATLab to track parameters of interest over developmental time. These parameters were developed as a means of detecting developmental trends in a large data set. The definitions of these parameters are as follows.

Phrase bout size. We counted the identifiable phrases in each singing bout (throughout this study, a *singing bout* is defined as continuous singing with a pause no greater than 250 ms; the overall results of this study were unchanged when this criterion was changed to either 200 ms or 300 ms). We counted the bouts that contained single phrases, phrase pairs, triplets, quadruplets, or quintuplets and expressed each as a ratio of the total number of bouts.

Pairwise syntax diversity. We used a normalized modification of Shannon's diversity index (Zar, 1999) to quantify the extent to which the 25 possible phrase pairings were represented on a given day of singing (Equation 1):

$$D = \frac{n \log n - \Sigma f(i) \log f(i)}{n \log 25},$$
(1)

where *n* is the total number of pairs sung on a given day and $f_{(i)}$ is the number of occurrences of the *i*th phrase pairing. This index has been used in a variety of ecological and communication contexts to quantify, for example, species diversity (Whittaker, 1972) or diversity of bottlenose dolphin whistle repertoires (McCowan, Hanser, & Doyle, 1999).

Emergence of phrase pairings present in final song. We measured the occurrence of a given phrase pair in crystallized song relative to the occurrence of all other phrase pairs beginning with the same phrase type on a given day. This parameter ranges from 0 (no occurrences of a given phrase pair) to 1.

Temporal coupling. Temporal coupling reflects the temporal gap between two phrase types. Our temporal coupling index is calculated as the crystallized interval between two sequential phrase types in a bout of song for an individual bird, divided by the median interval produced on a given day during development. This index approaches 1 as a bird approaches crystallization.

Statistical analyses. To test for early differences in pairwise syntax diversity among tutor groups, we averaged diversity scores over the first 10 days after tutoring for each bird and performed a Krukal-Wallis test to determine whether there was an overall difference among tutor groups. We then performed Mann-Whitney U comparisons between pairs of tutor groups, with Bonferroni correction for multiple comparisons. To determine the time at which birds underwent a switch from producing predominantly single phrases to producing predominantly longer bout lengths (see Table 1), we chose the earliest date for each bird at which single phrase production did not predominate and after which single phrase production did not predominate again for the remainder of ontogenetic time. We then averaged these dates (days after tutoring) across birds within a tutor group. To determine the timing of major changes in syntax diversity and temporal coupling (see Table 1), we chose the earliest date for each bird at which the parameter decreased (or increased in the case of temporal coupling), and continued to decrease (or increase) for the remainder of ontogenetic time (allowing for minor fluctuations), and averaged dates across birds within a tutor group. To determine timing of emergence of final pairings (see Table 1), we chose the earliest date for each bird at which production of the final pairing predominated and continued to predominate for the remainder of ontogenetic time and averaged dates across birds within a tutor group.

Table 1

Timing (Mean \pm 95% Confidence Interval Days Posttutoring and Date) of Major	Changes in
Syntactical Parameters for All Tutor Groups	

Tutor group	Phrase groupings	Syntax diversity	Emergence of final pairings (AB-BA)	Temporal coupling of final pairings
Full song				
Forward	219 ± 8.7	200 ± 12.6	175 ± 58.8	182 ± 18.8
Reverse	214 ± 7.2	182 ± 21.7	80 ± 70.3	170 ± 25.6
Phrase pairs				
Forward	236 ± 20.9	203 ± 29.3	196 ± 51.7	173 ± 25.2
Reverse	235 ± 47.9	172 ± 17.6	81 ± 71.3	181 ± 60.7
Single phrases	221 ± 10.8	194 ± 12.2	220 ± 16.2	197 ± 12.1
Isolates	219 ± 38.4	200 ± 20.4	202 ± 59.8	161 ± 28.7

Statistical differences in timing of changes in syntactical parameters between groups were assessed using Mann–Whitney U comparisons.

Results

Crystallized Songs

A spectrographic example of a typical white-crowned sparrow song, containing all phrase types from which tutor files were constructed, is shown in Figure 1. A detailed description of crys- F1 tallized songs produced by birds in the tutor groups (excluding isolate birds) described earlier is given in Plamondon et al. (2008). Briefly, birds tutored with full song crystallized songs consisting of three to five phrases, birds tutored with phrase pairs crystallized songs consisting of three to four phrases, and most birds tutored with single phrases crystallized songs consisting of three phrases. Birds tutored with forward- or reverse-order syntax produced songs that matched tutor syntax, whereas birds tutored with single phrases produced variable syntax; however, forward syntax predominated in these birds. Additionally, birds tutored with single phrases exhibited decreased proficiency at imitating phrase phonology relative to birds tutored with full song or phrase pairs. Isolate birds crystallized songs consisting of three to nine phrases that included whistles, frequency-modulated whistles, a note complex, trills, and buzzes (Figures 2a-f). Apart from whistles (A-type F2 phrases), none of the phrases present in the tutoring regimes of the other groups were included in the crystallized songs of isolate birds.

Developmental Trajectories

Spectrograms of vocalizations produced at various developmental time points by a representative bird from each tutor group are shown in Figure 3. Each bird (excluding isolate birds) produced F3 some number of primitive versions of what would eventually become its crystallized song beginning very early in development (Figures 3a-c); however, developmental trajectories did not consist of a straightforward refinement of these early song renditions and concurrent elimination of inappropriate renditions. Instead, birds from all groups produced many different syntactical combinations of varying numbers of phrases with variable timing for the majority of developmental time and eventually progressed to producing the single stereotyped songs described earlier. Some stud-

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Figure 1. Spectrogram of a white-crowned sparrow song used to generate tutor models. This particular dialect of white-crowned sparrow song consists of five phrases: a whistle (A), a trilled note complex (B), a high-pitched buzz (C), a lower pitched buzz (D), and a second note complex (E).

ied aspects of this progression differed among tutor groups, whereas others remained relatively constant. We present these details in the following sections.

Phrase Bout Size

We first examined how the grouping of different numbers of phrases changed over time. We calculated the proportion of identifiable phrase assemblages (ranging from single phrases to fivephrase sequences) that each bird produced on a given day and constructed a timeline for each bird. We defined an identifiable phrase assemblage as a sequence consisting entirely of phrases judged to be imitations of tutor phrases. Phrases that were embedded in unidentifiable subsong were included in these analyses; for example, a single identifiable phrase included in the middle of a bout of subsong was counted as a single phrase grouping. Timelines of means \pm 95% confidence intervals for each tutor group are presented in Figure 4.

Birds tutored with full songs or single phrases. Birds tutored with full songs (Figures 4a and 4c) or single phrases (Figure 4e) produced a high proportion of single phrases during approximately the first 210 days after tutoring (see Table 1), after which the number of single phrases decreased relative to the proportion of higher order combinations. This pattern did not differ between birds that received full song with phrases presented in a forward order and those tutored with full song in which phrases were presented in a reverse order (Figures 4a and 4c).

Birds tutored with phrase pairs. As with birds tutored with full song or single phrases, those tutored with phrase pairs produced predominantly single phrases early in development (Figures 4b and 4d). Unlike the other groups, however, these birds produced predominantly phrase pairs during a period in mid-plastic song (purple lines, Figures 4b and 4d). This period lasted approximately



Figure 2. Spectrograms of crystallized songs of birds raised in acoustic isolation. Isolate birds crystallized songs containing whistles, frequency-modulated whistles (wc04, first phrase; wc16, first and third phrases; wc18, second, fourth, and fifth phrases), a note complex (wc05, final phrase), buzzes (wc04, final two phrases), and trills (wc11 and wc16, final phrase).

F4



Figure 3. Spectrograms of vocalizations produced at various developmental time points by representative birds from four tutor groups. Spectrograms shown are from a bird tutored with full forward song (a), reverse-order pairs (b), single phrases (c), and an acoustically isolated bird (d). Numbers in parentheses indicate the bird's identification number, and numbers to the left of each spectrogram indicate days after tutoring. In the case of wc05 (d), which was not tutored, numbers to the left of each spectrogram (and all indications of days after tutoring for isolate birds in Figures 4–11) represent days elapsed from September 15 of the year of capture (see Method section). For early time points, song renditions shown are not typical of a bird's repertoire at that time (see the Results section) but were chosen to illustrate that each bird produced some renditions of what would eventually become its crystallized song very early in development.

30 days for birds tutored with forward-order or reverse-order phrase pairs ($203 \pm 9.0 \text{ days} - 235 \pm 10.2 \text{ days}$). At the close of this period ($\sim 235 \text{ days}$ after tutoring; Table 1), birds in both forward and reverse paired-phrase groups progressively produced higher order combinations, as in the other groups.

Isolate birds. Early in development, isolate birds, unlike those in other groups, did not show a strong bias toward producing predominantly single phrases (Figure 4f); for approximately 100 days posttutoring, similar numbers of single and paired phrases were produced. Although phrase-sequence length was more variable across birds in this group, the general progression of this parameter followed approximately the same time course as that in birds tutored with full song or single phrases. Birds produced primarily single and paired phrases to a point relatively late in development (\sim 220 days after tutoring; Table 1), at which point higher order combinations predominated.

Pairwise Syntax Diversity

Although birds from all groups produced a high proportion of single phrases throughout much of song development, they also produced phrase pairs and higher order combinations, even during early plastic song (see Figure 4). If instructive processes influence syntax development during the early plastic song stage, syntactical arrangements should largely reflect tutor information; birds that receive atypical syntax information—that is, phrases presented singly at 2.5-s intervals—during tutoring might show less pairwise syntactical diversity than birds that heard phrases in particular combinations. Alternatively, a selective model of syntax assembly would be supported if during the early plastic song stage birds produce a wide variety of syntactical arrangements, and this diversity is largely independent of the syntax information that birds received during tutoring; provided that birds heard all phrase types, they should combine these phrases in all possible syntactical arrangements. To investigate this issue, we examined the diversity of phrase pairings in all tutor groups (see the Method section) over developmental time.

Birds receiving tutor information—early development. The range of syntactic material (phrase pairings) produced immediately after tutoring varied among treatment groups (Kruskal-Wallis test: $H_2 = 14.34$, p = .0008; Figure 5). Specifically, post F5 hoc pairwise Mann–Whitney U comparisons revealed that birds tutored with full song and phrase pairs exhibited significantly more pairwise syntactic diversity within the first 10 days after tutoring than birds tutored with single phrases (full song tutored vs. single phrase tutored: Mann–Whitney U = 39, $N_1 = 15$, $N_2 = 7$, p <



Figure 4. Proportion of groupings of 1 to 5 phrases (mean \pm 95% confidence interval) versus days after tutoring. Relative proportions of phrase bout sizes are shown for birds tutored with full song (a and c), phrase pairs (b and d), and single phrases (e) and isolate birds (f). Phrases were considered to be grouped if less than 250 ms transpired between the end of one phrase and the beginning of the subsequent phrase. Purple lines indicate phases in which production of phrase pairs predominate.



Figure 5. Pairwise phrase syntax diversity (mean \pm 95% confidence interval) for birds tutored with full song (black), phrase pairs (hatched), and single phrases (striped) in the first 10 days after tutoring.

.005; phrase pair tutored vs. single phrase tutored: Mann–Whitney U = 32, $N_1 = 8$, $N_2 = 7$, p < .005). These differences were significant after Bonferroni adjustment for multiple comparisons (.05/2 = .025) and support an instructive role of acquired syntax information in the syntactical development of early plastic song.

There were no significant differences in the diversity of syntactic material in the first 10 days after tutoring between birds tutored with full song and birds tutored with phrase pairs (full song tutored vs. phrase pair tutored: Mann–Whitney U = 99, $N_1 = 15$, $N_2 = 8$, p = .87). Pairwise syntactic diversity at any time during development did not simply correspond to the amount of singing because there was no significant relationship between the diversity index and the number of phrase pairs sung on the same day (a measure of total song output), F(1, 32) = 0.16, p = .69, $r^2 = .0049$.

The low pairwise syntactic diversity exhibited by birds tutored with single phrases could result from these birds singing all five phrase types to which they were exposed in early development but combining them in fewer different combinations than birds from the other groups. Alternatively, these birds might sing fewer phrase types in early development than birds from the other groups, thereby limiting the potential number of different phrase combinations and lowering the syntactic diversity. Support for the latter alternative comes from our previous finding that birds tutored with single phrases crystallized fewer phrase types than birds tutored with full song or phrase pairs (Plamondon et al., 2008). To further explore this hypothesis, we examined the mean relative production of phrase types in birds tutored with full song (Figure 6a), phrase F6 pairs (Figure 6b), or single phrases (Figure 6c). We found that birds tutored with single phrases only produced three phrase types within the first 10 days after tutoring (they did not sing C or E



Figure 6. Relative production of phrase types (A, B, C, D, and E; mean \pm 95% confidence interval) versus days after tutoring. Birds tutored with single phrases did not produce C and E phrases during the first 10 days after tutoring and for the majority of development (c), whereas birds tutored with full song sang all five phrase types throughout development (a). Birds tutored with phrase pairs also sang all phrase types, with the exception of the E phrase early in development (b).

types; Figure 6c) and throughout the majority of developmental time. Birds tutored with complete or paired syntax information (full song or phrase pairs), however, produced more phrase types early in development (birds tutored with full song produced all phrase types, whereas those tutored with phrase pairs produced four phrase types; Figures 6a-b). Thus, it appears that the low syntactic diversity exhibited by birds tutored with single phrases early in development can be partially attributed to the finding that these birds produced fewer phrase types at this time.

To explore whether the reduced number of phrase types produced by single-phrase-tutored birds fully accounted for their low pairwise diversity scores, we recalculated diversity scores for these birds, normalizing by the maximum number of unique phrase pairs that can be produced with three phrase types (nine; we originally normalized by 25, the maximum number of phrase pairs that can be produced with five phrase types; see the Method section). We found that the average diversity score increased only marginally for these birds (.19 compared with .13) on renormalization. Because phrase-pair-tutored birds produced only four phrase types in the first 10 days after tutoring (allowing for a maximum of 16 unique phrase pairs), we renormalized their diversity scores as well and found that the average diversity score increased to an even greater degree (.67 compared with .57) on renormalization. Birds tutored with full song sang all five phrase types during the first 10 days of tutoring; hence renormalization was unnecessary for these birds, and the original calculated average diversity score of .52 (see Figure 5) can be compared with the other renormalized scores. Thus, the smaller number of phrase types produced by birds tutored with single phrases does not fully account for their reduced diversity scores.

Isolate birds—early development. Isolate birds could not be directly compared with the other groups in this analysis because their pairwise diversity scores were based on the phrases that they ultimately produced rather than the five types of tutor phrases heard by other groups. As mentioned earlier, isolate birds did not produce any phrases other than whistles that exhibited any obvious similarity to the tutor phrases used in this study; they therefore did not assemble any syntactic combinations consisting of these phrases.

Birds from all groups-developmental progression. Although pairwise syntactic diversity immediately after tutoring was related to syntax tutor models, individual patterns of diversity over the course of development varied widely, independent of the tutor group to which a bird belonged. Birds from all groups (including isolates), however, exhibited a relatively rapid decline from a high level of diversity to a lower level of diversity in late plastic song. For 82% of birds, this decline occurred from the highest level of diversity attained. The onset of this decline occurred at approximately the same time in late plastic song for all groups (see Table 1).

Emergence of Phrase Pairings Present in Final Songs

The pairwise diversity measures indicate that birds across groups in early plastic song assembled phrases in many possible pairings. We next asked whether the phrase pairings present in tutor models were preferentially produced during this stage and how the relative proportion of correct (tutor) and incorrect phrase pairings changed during song development.

Birds tutored with forward-order syntax. A and B phrase types in birds tutored with full forward song occupied the first and second positions in the crystallized songs of these birds. Incorrect phrase pairings included BA pairs (reverse of tutor order) and pairings that began with A and ended with any other phrase type (AX). On the 1st day after tutoring, although incorrect pairings of the AX type predominated, these birds produced a substantial proportion (approximately 35%) of correct pairings (AB; Figure 7a; a pairing was defined as two successive phrases separated by F7 less than 250 ms; see the Method section). Incorrect pairings of the XB type (X being any phrase type other than A) were rare (data not displayed). Incorrect pairings representing the reverse of tutor order (BA pairs; light blue trace) also occurred infrequently. The proportion of correct pairings began to rise at approximately 90 days after tutoring but did not exceed the proportion of incorrect pairings until approximately 180 days (see Table 1). At this point, the proportion of correct pairings continued to rise as birds crystallized the correct AB pairing. Although there is a lack of early data for birds tutored with forward-order phrase pairs, for whom AB pairs also occupied the first position in crystallized song, it appears that the trend is similar, with correct pairings exceeding incorrect pairings at approximately 190 days after tutoring (Figure 7b; Table 1).

The predominance of the AB syntactical arrangement over the reverse syntax (BA) even in early plastic song could reflect the species-typical tendency for white-crowned sparrows to begin songs with whistles. We next asked, therefore, whether birds tutored with reverse syntax (BA) also showed an early bias toward producing the tutor syntax.

Birds tutored with reverse-order syntax. Birds tutored with reverse-order syntax song developed reverse phrase order, in which BA represented the last phrase pair of song rather than the first. Unlike birds tutored with forward-order syntax, these birds produced predominantly (60%) tutor-order (or correct) combinations almost immediately after tutoring (Figure 7c); that is, birds produced BA pairings more frequently than the sum of all other pairings in which B was the first phrase. Incorrect pairings of the BX type represented approximately 30% of pairings immediately after tutoring, whereas incorrect pairings reversed from tutor order (AB pairs; light blue trace) occurred more frequently immediately after tutoring than in birds tutored with forward-order syntax (20% vs. 0%; Figures 7a and 7c). Birds tutored with reverse-order phrase pairs showed a pattern of syntax development that was highly similar to that of birds tutored with full reverse song (Figure 7d). Thus, birds tutored with reverseorder syntax established correct phrase pairings at a significantly earlier time than those tutored with forward-order syntax (Mann-Whitney $U = 81, N_1 = 12, N_2 = 11, p < .002$; Table 1). A substantial number of incorrect combinations continued to persist throughout much of development, but their production never predominated for any substantial amount of time. As with the other groups, birds eventually eliminated incorrect phrase combinations. Thus, although the species-typical tendency to begin songs with whistles was reflected in the production of AB pairings, these birds nevertheless predominantly combined these two phrases in the tutor order (BA) in early plastic song.

Birds tutored with single phrases. Birds that were tutored with single phrases crystallized songs that began with A-type phrases. We worked backward from the crystallized songs of these birds and determined how the syntactical pairings in their final



Figure 7. Emergence of phrase pairings of A and B phrase types. Proportion of tutor- or crystallized-order (dark blue lines), nontutor- or noncrystallized-order (red lines), and reverse-order (light blue lines) phrase pairings of A and B phrase types (mean \pm 95% confidence interval) over developmental time for birds tutored with forward-order syntax (full song and phrase pairs; a–b), reverse-order syntax (full song and phrase pairs; c–d), and single phrases (e) and isolate birds (f).

songs emerged over time. Figure 7e shows the progression toward the syntactic pairing present in the crystallized songs (first two phrases) of birds tutored with single phrases (mean \pm 95% confidence interval). As with birds tutored with full song and phrase pairs, these birds produced phrase pairings in early development that were present in their crystallized songs; however, the reverse syntactical arrangement was nearly as common (light blue trace, Figure 7e). As with birds tutored with forward-order syntax, pairings not present in crystallized song predominated in early development and continued to do so until approximately 220 days after tutoring (see Table 1).

Isolate birds. Birds that were not tutored (isolates) showed a temporal pattern of syntax development similar to that of birds tutored with single phrases (Figure 7f). The phrase pair that was present at the beginning of each bird's crystallized song was only slightly more common in early plastic song than the reverse arrangement, whereas pairings beginning with the initial phrase in their crystallized songs and ending with any other type of phrase characteristic of those in crystallized song predominated until approximately 220 days after tutoring (see Table 1).

Other phrase pairings. As noted, the A and B phrase combination occurred in the initial position of song for birds tutored

with forward-order syntax, whereas it occurred in the final position for birds tutored with reverse-order syntax. The early bias for correct combinations of B and A phrases seen in birds tutored with reverse-order syntax was also present for combinations of E and D phrases (Figures 8b-8c); the ED phrase combination occurred in F8 the initial position of song for these birds. Birds tutored with forward-order syntax, for whom the DE combination occupied the final position of song, exhibited a trajectory more similar to that shown for their AB phrase pairings, with incorrect pairings predominating throughout much of their development (Figures 8a and 7a-b). Although an early bias for assembling correct combinations was seen in the initial (ED) and terminal (BA) phrase combinations of birds tutored with reverse song compared with birds tutored with forward song, a similar pattern was not present for the intermediate combinations of B and C phrases (see Figure 9) and C and D phrases (see F9 Figure 10). The proportions of correct and incorrect combinations F10 of B and C phrases were approximately equal throughout early development for birds tutored with either forward-order (Figures 9a-b; BC and BX) or reverse-order (Figure 9c; CB and CX) syntax. Birds tutored with forward-order syntax produced approximately equal proportions of correct and incorrect combinations of C and D phrases in early development (Figures 10a-b; CD and



Figure 8. Emergence of phrase pairings of D and E phrase types. Proportion of tutor-order (dark blue lines), nontutor-order (red lines), and reverse-tutor order (light blue lines) phrase pairings of D and E phrase types (mean \pm 95% confidence interval) over developmental time for birds tutored with full forward-order syntax (a) and reverse-order syntax (full song and phrase pairs; b–c). Birds tutored with forward-order phrase pairs did not crystallize E phrase types and therefore are not shown.

CX), whereas birds tutored with reverse-order syntax produced predominately incorrect combinations of C and D phrases (DX) in early development for (Figure 10c). As with pairings in the initial and terminal positions, productions of pairings reversed in order

from the tutor sequence were rare throughout development for birds receiving syntax information in either a forward or a reverse order (Figures 9 and 10, light blue traces). In all groups, production of correct pairings predominated with similar timing to that seen



Figure 9. Emergence of phrase pairings of B and C phrase types. Proportion of tutor-order (dark blue lines), nontutor-order (red lines), and reverse-tutor order (light blue lines) phrase pairings of B and C phrase types (mean \pm 95% confidence interval) over developmental time for birds tutored with forward-order syntax (full song and phrase pairs; a–b) and reverse-order full song (c). Birds tutored with reverse-order phrase pairs did not crystallize CB phrase pairings and therefore are not shown.



Figure 10. Emergence of phrase pairings of C and D phrase types. Proportion of tutor-order (dark blue lines), nontutor-order (red lines), and reverse-tutor order (light blue lines) phrase pairings of C and D phrase types (mean \pm 95% confidence interval) over developmental time for birds tutored with forward-order syntax (full song and phrase pairs; a–b) and reverse-order full song (c). Birds tutored with reverse-order phrase pairs did not crystallize DC phrase pairings and therefore are not shown.

for the initial pairing in birds tutored with forward syntax, birds tutored with single phrases, and isolate birds (130–180 days after tutoring; Table 1; Figure 7). Pairings subsequent to the initial pairing for birds tutored with single phrases or isolate birds followed a pattern similar to that seen for the initial pairing and are not shown.

Temporal Coupling of Phrase Pairings

Song syntax is characterized not only by the ordering of phrases within a song, but also by the precise timing between phrases. How does the timing between adjacent phrases in song change during development? Is this development influenced by the type of syntax information that birds received during tutoring?

Birds tutored with forward-order syntax. Figure 11a illustrates the developmental trajectory of temporal coupling values (normalized using the values present in the crystallized song of each bird; see the Method section) of the AB phrase pairing for birds tutored with full forward song. These phrase types remained relatively loosely coupled throughout much of development, until approximately 180 days after tutoring (see Table 1). Subsequently, the temporal gap between A and B phrases progressively decreased until crystallized timing $(33 \pm 4.6 \text{ ms})$ was reached. This late progression from relatively loose temporal coupling to the coupling seen in crystallized song was also observed in birds tutored with forward-order phrase pairs, with a progression toward crystallized timing beginning at ~ 173 days posttutoring (Figure 11b; Table 1). Birds tutored with phrase pairs (forward and reverse order) did decrease the interval between crystallized pairings at a slightly earlier time than birds tutored with full song

(Figures 11a–d); however, this difference was not statistically significant (Mann–Whitney U = 21.5, $N_1 = 16$, $N_2 = 8$, p = .15).

Birds tutored with reverse-order syntax. As discussed earlier, birds tutored with reverse-order syntax produced predominantly correct combinations of B and A phrases early in development. Because these birds produced such a large proportion of tutor-matched combinations so early in development, one might expect that a crystallized timing between these phrases would emerge more rapidly. This was not the case, however. Temporal coupling of crystallized combinations followed a trajectory similar to that seen for all other groups (Figures 11c–d).

Birds tutored with single phrases and isolate birds. Developmental trajectories tracking temporal coupling of the initial phrase pairing in birds tutored with single phrases and isolate birds are shown in Figures 11e–f. Both of these groups also exhibited relatively loose temporal coupling of phrase pairings that eventually made up their crystallized songs throughout much of development. Birds from these groups began their progression toward crystallized timing at 197 \pm 3.7 days and 161 \pm 31.3 days after tutoring (birds tutored with single phrases and isolate birds, respectively; Table 1), timing that did not differ from that seen in birds tutored with forward-order syntax (Mann–Whitney U = 78, $N_1 = 10$, $N_2 = 11$, p = .1).

Other phrase pairings. Ontogeny of temporal coupling of phrase pairings subsequent to the initial pairing for all groups followed a similar trajectory to that seen for the initial phrase pair. Thus, for all groups, birds exhibited loose and variable temporal coupling early in development for all phrase pairings present in their final songs. Progression toward crystallized timing in all groups and for all phrase pairings occurred with similar timing late in development (see Table 1).

F11

 a) Full Forward Tutored AB b) Forward Pairs Tutored AB Temporal Coupling of Phrase Pairings 160 240 80 160 240 c)Full Reverse Tutored BA d) Reverse Pairs Tutored BA 160 240 80 160 240 8່0 đ e) Singles Tutored 1-2 f) No Tutoring 1-2 0.8 0.6 0.4 0.2 240 240 160 160 Days Post-Tutoring Days Post-Tutoring

Figure 11. Temporal coupling of A and B phrase types. Temporal coupling was measured over development for birds tutored with forward-order syntax (full song and pairs; a-b), reverse-order syntax (full song and phrase pairs; c-d), and single phrases (e) and isolate birds (f).

Discussion

This study provides the most extensive analysis of syntax development in white-crowned sparrows to date and is the first to investigate how different levels of syntax information in tutor models might influence this development. We found that regardless of the nature of tutor information, birds predominantly produced single (temporally isolated) phrases during the early plasticsong stage. This bias continued until at least 200 days after tutoring, except in birds tutored with phrase pairs; these birds produced more phrase pairs as the proportion of single phrases decreased, with pairs predominating at approximately 200 days after tutoring. Second, birds that received complete or paired syntax information during tutoring sang a greater diversity of phrase pairings than birds tutored with single phrases. Although birds that received complete or paired syntax information during tutoring combined phrases in a variety of syntactical arrangements, they rarely paired phrases in an order that was reversed from the syntax in tutor models; this was true even in the 1st week after tutoring. Birds tutored with reverse-order syntax produced predominantly correct (tutor-order) pairs of initial and terminal phrase pairings earlier in development than birds from other groups. Finally, major changes in syntax occurred at approximately the same time for birds in all groups. In the next paragraphs, we discuss these findings in relation to current theories of song learning, in particular instructive and selective processes.

Our findings are generally consistent with earlier work showing that selective forces are important in song development but suggesting that instructive processes also play important roles. In support of the selective model, birds tutored with complete or paired syntax information combined phrases in a variety of ways, ultimately eliminating those that did not match the tutor syntax. Surprisingly, however, birds that were tutored with all phrases, but presented singly, showed less diversity of phrase pairings in early plastic song than those that received more complete syntax information. Because these birds did not receive phrase-order information during tutoring, we expected that they would combine these phrases in all possible orders, that is, exhibit and maintain the highest degree of syntax diversity. This was not the case. In addition, these birds showed impaired development of some phrase types (Plamondon et al., 2008; Figure 5). These birds only produced three of the five possible (tutored) phrase types during the first 10 days after tutoring, contributing to low pairwise diversity scores. Moreover, when we normalized diversity scores in these birds to reflect the reduced number of different phrase pairings possible with only three phrase types, diversity scores were still much lower than those of birds from other groups. We interpret these results to indicate that syntax-related tutor information acts in an instructive manner to guide phrase development and, furthermore, that particular pairings of phrases emerge in birds tutored with phrase pairs and full song as the result of tutor syntax information.

Birds that received paired or complete syntax information during tutoring showed an early bias toward combining phrases in the correct order. Within the 1st week after tutoring, the earliest period analyzed, birds rarely coupled phrases in an order opposite that in the tutor models. Birds that were tutored with single phrases, however, combined phrases in forward and reverse order (with respect to the order in their crystallized song) with equal frequency until late in plastic song. It appears, therefore, that acquired template information about phrase syntax acts very early in song development to guide motor pattern development, including the order of phrase coupling. Thus, syntax development appears to occur at a stage wherein phrase structure is still relatively poorly matched to that in tutor models. It is noteworthy, however, that birds from all groups (excluding isolates) produced recognizable imitations of at least some phrase types from the earliest measured developmental time point. Although early imitation of phrases has been observed in wild white-crowned sparrows (Baptista, Bell, & Trail, 1993; DeWolfe & Baptista, 1995; DeWolfe, Baptista, & Petrinovich, 1989), this finding has not previously been reported for lab-reared white-crowned sparrows.

Immediately after tutoring, in addition to the tendency to produce more correct than reverse-order combinations, birds tutored with reverse-order syntax also produced many more BA or ED (correct) pairings than the sum of all other pairings beginning with the same phrase. This bias appeared significantly earlier in developmental time than for birds tutored with forward-order syntax. This result was surprising because the introductory whistle appears to be a species-typical feature of white-crowned sparrow song that has been shown to facilitate song acquisition in this species (Konishi, 1978; Marler, 1970; Soha & Marler, 2000). Reverse-order tutor information conflicted with this species-typical tendency, and yet birds tutored with reverse-order syntax assembled predominantly correct BA rather than BX pairings earlier than correct AB

rather than AX pairings that predominated in birds tutored with forward-order syntax. It could be the case that if acquired information directs phrase pairings differently from innate tendencies, the developmental trajectory is altered. The relative position of certain phrase types may play an instrumental role in determining the time course of these trajectories. This raises the possibility that this finding was specific to the white-crowned sparrow dialect used to tutor birds in our study; white-crowned sparrows tutored with other dialects containing different phrase orders may not show this ontogenetic difference in the assembly of reverse versus natural phrase order. Future studies could address this possibility.

Acquired template information also appears to play instructive roles later in song development. Birds in all tutor groups produced a high proportion of single phrases beginning early in development and continuing to approximately 220 days after tutoring. This was true for birds tutored with phrase pairs as well; however, this period was truncated in these birds to include a phase wherein production of phrase pairs predominated. Presumably, exposure to phrase pairs during the sensitive period biased birds toward producing predominantly phrase pairs at a point later in development. Birds tutored with phrase pairs also appeared to be slightly accelerated in their temporal coupling of phrase pairings compared with birds from other groups (see Figure 11). This acceleration could again be the result of the specific tutor models that these birds heard (phrase pairings), which enabled them to decrease the interval between phrase pairings earlier in development.

Although tutor information can influence learning trajectories, it is perhaps surprising that many aspects of syntax development, such as the timing of major changes and the tendency for all birds to produce predominantly single phrases throughout much of development, remained relatively invariant across tutor groups despite the differential exposure to syntax information. This was true even for birds that received atypical syntax information (singlephrase-tutored birds) or no syntax information (isolate birds; in the case of these birds, no tutoring information whatsoever), which suggests that these features of song development may be guided by species-typical ontogenetic patterns. These features of song development may not necessarily require a sensory representation but may instead result from physiological processes, such as the actions of circulating steroid hormone levels on motor pattern generators (Brenowitz, 2004; Meitzen, Moore, Lent, Brenowitz, & Perkel, 2007).

One such feature of song ontogeny that remained consistent across all groups was the timing of major changes in song structure that occurred late in development. A variety of syntactical parameters that we measured, including phrase bout size, phrase pair diversity, emergence of crystallized phrase pairings, and timing of crystallized phrase pairings, showed rapid and marked changes in a progression toward crystallized song during approximately the same time period in late plastic song (see Table 1). These birds were kept on natural photoperiods, and there is abundant evidence that photoperiod influences gonadal cycles in birds (Baptista &

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Gaunt, 1994; Brenowitz, 2004; Farner & Lewis, 1971; Lofts & Murton, 1968; Wingfield & Farner, 1978). Elevated circulating levels of testosterone in turn act on song control nuclei and induce song stereotypy and song crystallization in white-crowned sparrows and other species of songbirds (Ball et al., 2004; Brenowitz, 2004; Marler, Peters, Ball, Dufty, & Wingfield, 1988; Meitzen et al., 2007; Nottebohm, 1981; Tramontin & Brenowitz, 2000; Whal-

ing, Nelson, & Marler, 1995; Whaling, Soha, Nelson, Lasley, & Marler, 1998). Changes in the syntactical structure of late plastic song, therefore, most likely come about as a consequence of a testosterone-induced drive to produce a stereotyped song.

Another feature of syntax development that remained constant across all tutor groups was the tendency for birds from all groups to produce a high proportion of identifiable phrases in isolation from other identifiable phrases relatively late into development (although, as described earlier, this phase is truncated in birds tutored with phrase pairs). This finding was surprising. Why do birds whose final songs consist of groupings of three to six phrases produce predominantly single phrases for such a prolonged period of time? One possibility is that in early development, the unidentifiable subsong in which these phrases can be embedded consists of precursors to phrases that will eventually be coupled with the identifiable phrase. Such a strategy is observed in some zebra finches, which assemble global imitations of tutor song and over time refine the phonology of the constituent precursor syllables (Liu, Gardner, & Nottebohm, 2004). This does not appear to be the case in white-crowned sparrows, however. At a very early stage in development, all tutored birds produced identifiable primitive versions of all phrase types (with the exception of birds tutored with single phrases, which had fewer phrase types in their early songs). A particular syllable of subsong was not consistently coupled with a particular phrase type and, moreover, phrase types were often translocated in song as birds practiced a variety of syntactical combinations (Plamondon et al., ????). In fact, these findings suggest that early in development, birds may be practicing syntax by inserting individual precursor syllables in different parts of a song, similar to what is observed later in development, because birds practice many different identifiable syntactical combinations. In this study, we focused primarily on identifiable phrases; however, a detailed study of all syntactic material, including subsong and other improvised material, could shed further light on ontogenetic processes.

A second possibility that may explain why birds maintain isolated phrases late in development is that birds benefit from a repertoire of "uncoupled" phrases. Phrases that are repeatedly sung in specific syntactical combinations may become relatively fixed as sensory and motor circuitry are established over the course of development. A "database" of uncoupled phrases might be useful for exploring a syntactical variety of higher order combinations without committing to a specific configuration and thus aid the bird in remaining syntactically plastic later into development. Such plasticity appears to be important in the context of social interactions late in development because sparrows, through a process of action-based learning, selectively eliminate songs that do not closely match those of their neighbors (Baptista & Morton, 1988; DeWolfe et al., 1989; Marler & Peters, 1981; Nelson, 1992, 2000). This behavior suggests a general learning rule that favors plasticity of song syntax late into development.

Although isolate birds produced a high proportion of single phrases throughout development, they also produced a higher proportion of phrase pairs and triplets early in development than birds that received tutor syntax information. These birds tended to string together sequences of whistles and other innate phrases early in development; because many of these phrases became incorporated in their final songs, they were counted early in development as recognizable sequences of phrases. Birds from all other groups tended to string together apparently innate phrases throughout development as well, but because these phrases were never incorporated into their final songs, they were not included in the analysis of phrase bout size.

Birds from all groups, therefore, produced single phrases throughout much of development, but all birds eventually crystallized songs consisting of three to six phrases. This tendency has previously been observed and reported in isolate white-crowned sparrows (Marler, 1970; Nelson & Marler, 1994; Soha & Marler, 2001a). Tutoring with models that conflicted with the three- to six-phrase tendency (i.e., single phrases and phrase pairs) did not result in production of one- or two-phrase crystallized songs, suggesting that tutor information cannot easily override this tendency. Birds tutored with full songs, however, included more phrase types in their final songs than pair-tutored birds, which in turn crystallized more phrase types than birds tutored with single phrases (Plamondon et al., 2008), indicating that instructive processes can influence the number of phrases in crystallized song to some degree. Additionally, there appeared to be a tendency to include some species-typical complexity in crystallized songs. Birds tutored with single phrases in this and a previous study by Soha and Marler (2001b) included a variety of phrase types in their final songs. Isolate birds in this study also did not crystallize songs of single repeated whistles (a phrase that this species can produce without tutoring; Konishi, 1978; Marler, 1970) but combined whistles of different pitches, frequency-modulated whistles, trills, and buzzes to assemble complex songs (see Figure 2), thereby satisfying a potential phrase-diversity drive.

Although early syntax information appears to play an instructive role in the development of syntactical structure, our data suggest that selective forces guide syntax development as well. Birds from all groups produced many syntactical combinations beyond those with which they had been tutored and continued to do so late into plastic song. Syntax diversity scores dropped during the late stages of development, indicating that birds were winnowing their repertoires. Thus, in this study, we found evidence for both instructive and selective processes. Marler (1997) proposed three theoretical models for song learning, one of which suggested that instructive and selective processes could work in concert to guide song learning, perhaps at different stages of development. Our data support this integrated model. Several neurophysiological studies have been interpreted to support either instructive or selective models of song learning (Adret & Margoliash, 2002; Bottjer & Troyer, 2001; Solis et al., 2000; Volman, 1993). Additional physiological studies could shed further light on the role of instructive and selective processes, although, as has been pointed out, the distinction between these two models may be somewhat difficult to discriminate neurophysiologically (Margoliash, 2002).

Finally, it is important to address the possibility that differences in ontogenetic trajectories among tutor groups that we interpret as resulting from differential exposure to syntax models are instead the result of decreased attention among birds to tutor models containing atypical syntax information. Although we cannot entirely rule out this possibility, we believe that it does not constitute the most straightforward explanation of our results. For example, birds tutored with phrase pairs persisted in producing pairs longer than birds from other groups and produced predominantly phrase pairs for a period late in development (see Figure 4); this presumably occurred because birds were tutored with phrase pairs, and it would be difficult to attribute to a lack of attention to tutor models. Similarly, birds tutored with single phrases showed reduced pairwise syntax diversity immediately after tutoring compared with the other groups and showed no bias toward final over reverse-order pairings early in development, whereas birds from other groups produced more correct than reverse-order phrase pairs early in development. Because the tutor models presented to single-phrasetutored birds contained no pairwise information and therefore no information about correct or reverse-order pairings, it is again difficult to imagine how a lack of attention to these models could contribute to these findings. We argue instead that the tutor models themselves (and the information contained or not contained therein) contribute to these aspects of song development.

It has been observed in zebra finches that some birds assemble their final syntax combinations via serial repetition of a single precursor syllable that is modified to give rise to different syllables (Liu et al., 2004; Tchernichovski et al., 2001). Others assemble global imitations of tutor song and over time refine the phonology of the constituent precursor syllables (Liu et al., 2004). Juvenile chipping sparrows produce several precursor songs, each consisting of a single syllable, and subsequently refine the syllable structure in a single song that becomes crystallized (Liu & Nottebohm, 2007). In these strategies, the global syntactical structure of song is present from a very early developmental time point. Whitecrowned sparrows appear to differ from these two species in that syntax remains variable throughout much of development. The majority of our birds produced precursors to specific phrase types that were subsequently arranged in a variety of syntactical combinations. Over time, phrase phonology was refined, and inappropriate syntactical combinations were eliminated. Thus, syntax and phonology appear to develop in parallel in white-crowned sparrows.

These observed differences among species might reflect differences in tutoring protocol and opportunities for social interaction, or they may be a reflection of species-specific differences in song learning trajectories or song function. For example, white-crowned sparrows are a seasonally breeding species that use song in territorial interactions, whereas zebra finches may breed year round if conditions are favorable, breed in colonies, and do not establish individual territories (Zann, Morton, Jones, & Burley, 1995). The prolonged syntax plasticity observed in this study could be related to sparrows' behavior in the wild, where birds selectively eliminate those songs that do not match those of their neighbors on their breeding territories, in a process of song sharing that is thought to be important in territorial success (Baptista & Morton, 1988; Beecher, Campbell, & Nordby, 2000; DeWolfe et al., 1989; Marler & Peters, 1981; Nelson, 1992, 2000). The timing of large-scale changes toward crystallization in syntactical parameters observed in this study corresponded roughly to the time at which migratory montane white-crowned sparrows arrive at their breeding grounds (Hahn, Sockman, Bruener, & Morton, 2004). Other differences among species include the length of the developmental sensorimotor period (9 months in white-crowned sparrows compared with 60 days in zebra finches; Tchernichovski et al., 2001) and social interactions. Ontogenetic studies in varying social conditions and in other species reflecting differences in open versus closed learners, developmental period lengths, and repertoire sizes would be informative in evaluating the aspects of song development that are

more general, those that are species specific, and those that can be overridden by specific social or acoustic information.

Comparative studies would also be informative in formulating more general theories relating to the development of communication behavior. Songbirds and humans undergo similar developmental trajectories in the course of acquiring their communication signals, progressing from unstructured vocalizations (subsong or babbling) to more refined signals. An unresolved question in human language development concerns the degree to which acquired elements of language are present during the babbling stage of vocalization (e.g., Macken, 1992; MacNeilage, Davis, & Matyear, 1997). This study's results suggest that in white-crowned sparrows, imitation from tutors occurs very early, during the subsong stage of development. Although recognizable imitations of tutor phrases do not constitute the majority of vocalizations at this stage, they are nevertheless present. Furthermore, our results suggest that acquired information can influence developmental trajectories in specific ways, but that these trajectories are also constrained by species-typical parameters. These and other findings may be useful in formulating and testing hypotheses on the influence of acquired information on speech development, thus furthering the exploration of parallels and differences in vocal ontogeny between humans and songbirds.

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