

Juvenile zebra finches can use multiple strategies to learn the same song

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Contributed by Fernando Nottebohm, October 29, 2004

Does the ontogeny of vocal imitation follow a set program that, given a target sound, unfolds in a predictable manner, or is it more like problem solving, with many possible solutions? We report that juvenile male zebra finches, *Taeniopygia guttata*, can master their imitation of the same song in various ways; these developmental trajectories are sensitive to the social setting in which the bird grows up. A variety of vocal developmental trajectories have also been described in infants. Are these many ways to learn unique to the vocal domain or a hallmark of advanced brain function?

learning strategy | social influence | vocal learning | zebra finch

Vocal ontogeny in songbirds provides a good model for studying how a complex set of learned vocal signals is acquired (1–4). The young bird must solve two problems. The first one is to identify and commit to memory the model it will imitate. The second one is how to achieve this imitation. The solution to the second problem, which is the subject of this report, could occur in various ways. For example, the young, naive brain could have at its disposal the program for all sounds used by that species, and then imitation would be a simple process of selection (5). Or there could be for each class of adult sound an unlearned starting point or prototype that is similar for all individuals and that then is modified until a close match with the model is achieved (4). A further possibility is that early vocal ontogeny unfolds as a learning exercise that acquaints the young brain with a range of vocal tract positions and their acoustic consequences; experience gleaned in this manner can then be used to imitate a chosen sound. These three possibilities need not be mutually exclusive, and there may still be others. Thus, there is no compelling logic that tells us, in advance, how vocal imitation will proceed in the young vocal learner. Similarly, we do not know whether every member of a species learns its song in the same way. If the answer is yes, then the trajectory followed by any one individual would be akin to the unfolding of a preset program, with little room for creativity or unexpected solutions. Conversely, if each individual is capable of following a number of different trajectories to achieve a same imitation, then the cognitive level of the task would seem greater. We used juvenile male zebra finches to explore these issues.

Zebra finches are highly social songbirds that breed colonially. In nature, male juveniles learn their songs by imitating that of their father or other adult males with whom they interact, often copying different parts of the song from different adults (6, 7). In the laboratory, juvenile males acquire and develop their songs between 20 and 80 days of age, a time known as the sensitive period for vocal learning. This period includes two partially overlapping phases. During the first phase, from 20 to 50 days, a juvenile male acquires, soon after fledging, the sensory memory of the song it will imitate (8). Observations we report here suggest that midway during this same period, the second phase, vocal imitation, gets under way. This second phase starts in the context of the soft, highly variable and poorly structured sounds of subsong. As subsong becomes more frequent and louder, it is gradually modified into recognizable units of sound (“syllables”) separated by silent gaps, and this more structured, yet still variable sound is called “plastic song”; over time the recogniz-

able units become more and more like the syllables of the song the bird is striving to imitate, and the song becomes more stable. Sometime between days 80 and 90 the by now sexually mature male produces its song with a degree of stability that approaches that of older adults. This song changes little after this point. The entire process that culminates with stable imitation of the model requires auditory feedback (9).

Materials and Methods

Sound Recording. Juveniles reared in a family setting shared the cage with their parents and siblings. They were in a room that had other cages of this type. One of us observed and recorded the singing behavior of each sibling male for 6–7 h each day from day 35 to day 50 after hatching (mostly at 0730–1230 and 1600–1800 hours). The early subsong (days 20–34) and advanced plastic song (days 50–60) were recorded every other or every third day. The style of singing did not seem to differ during the day. The stage during which serial repetition of sound is most commonly used usually lasts ≈ 5 days. A Marantz (Itasca, IL; model 221) tape recorder was used to record the songs of birds kept in a family setting. Sound-triggered recording software was used to record automatically for 7 h each day (0830–1530 hours) the songs of juveniles housed individually with an adult male in a sound-proof chamber.

Similarity Measurements. We measured the similarity (“similarity score”) between two songs or two syllables by using the default setting of the latest update of SOUND ANALYSIS 3.28 software (10). In short, this procedure can detect the similarity of two songs or two syllables on the basis of pitch, frequency modulation, Wiener entropy, and spectral continuity. The similarity score estimates the proportion of sound in the song model for which there is a close correspondence in the pupil’s song (10) or the proportion of sound that bears such close correspondence between two syllables.

Quantifying the Incidence of Serial Repetitions. A song was defined as a stream of sounds preceded and followed by a silent interval of >0.5 s; in the literature, this would correspond to a “song bout”; however, with our definition, it also applies to subsong. For each song with more than three consecutive syllables, the first syllable was compared with the second one (see below), and then the second syllable was compared with the third syllable, and so on. A song was considered to show serial repetition if three or more consecutive syllables had a similarity score $>75\%$, a phenomenon that rarely occurs in subsong or adult song. Had we accepted lower levels of similarity, then the criterion for serial repetition would have become too inclusive to be of interest. Initially we collected 100 s of song (mostly between 1000 and 1200 hours) every other day from each of six males (from three clutches) between posthatching days 30 and 60, and then we calculated the percentage of songs that included serial syllable repetitions. Then, for each of 23 males with similar song devel-

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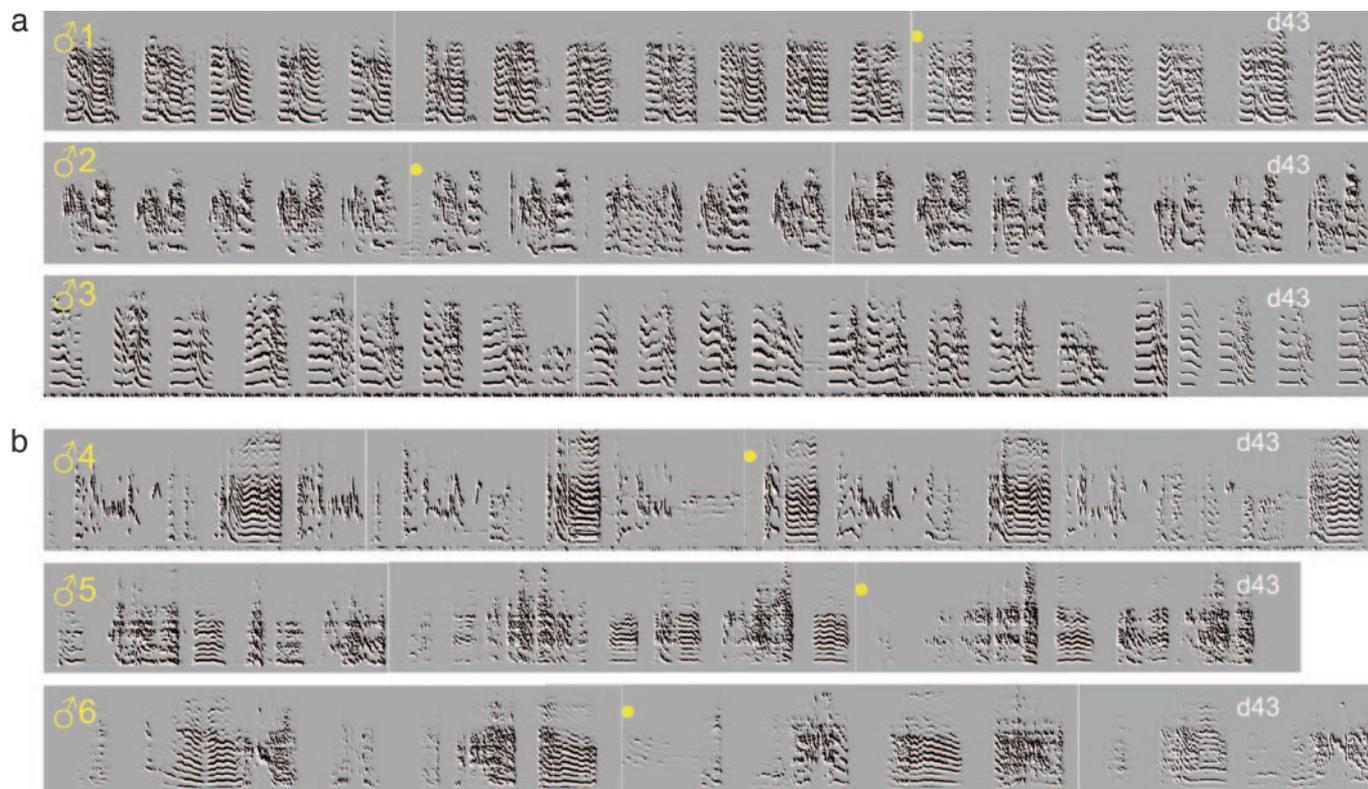


Fig. 1. This figure uses time-frequency analysis (10) to illustrate the striking difference in strategy followed by two groups of 43-day-old zebra finch juvenile males; birds in one group (a) produced serial repetitions of a single syllable type; birds in the other group (b) exemplify the early rise of a motif-centered strategy. Time is on the horizontal axis, and frequency is on the vertical axis. Shown for each bird is a sequence of sounds and pauses just as they were delivered, except for the silent interval between consecutive songs, which is not shown. Boundaries between consecutive songs are indicated by yellow dots. The way in which these two strategies emerge during ontogeny is shown in greater detail in Fig. 2.

opmental schedule, songs were collected at three different ages: 30–35 days (early subsong), 40–45 days (early plastic song), and 55–60 days (advanced plastic song). We used for sound analysis the first 100 s of song from each day's recordings (mostly between 1000 and 1200 hours) that were not overlaid by the vocalizations from other birds and used this sample to estimate for each bird the percentage of songs that showed serial repetition on that day (see Fig. 5).

Results

Multiple Strategies for Vocal Imitation. Our first evidence that zebra finches have multiple strategies for mastery of a vocal imitation came from visual inspection of the sound spectrographic record of song ontogeny in 37 family-reared juvenile zebra finches from 15 different clutches. These birds were kept, until 90 days of age, in cages that they shared with their parents and siblings. The term “strategy” is used here in a descriptive manner.

The two main strategies highlighted in Fig. 1 were obvious from the initial visual analysis. Early subsong, which starts during posthatching days 20–35 but most commonly around day 30, was similar in all juveniles, but 9–10 days after the beginning of subsong, a difference in how plastic song evolved could be seen among individuals. The developmental course of this difference is shown in greater detail in Fig. 2. In the “serial repetition” strategy ($n = 18$), an approximation to one syllable of the model is repeated many times (4). Often, but not always, different syllables from the final imitation emerge, through modification, from repetitions of the single syllable; they do so already in the order, relative to each other, in which they will appear in the adult song (4). So, for example, four different syllables from bird 1's successful imitation of the model song evolved from the initial

repetition of a same early syllable that was very similar to the model's syllable A. The serial repetition stage lasted in this bird ≈ 5 days, with some infrequent recurrence of serial repetition thereafter.

The second, “motif” strategy ($n = 19$ males) is exemplified by birds 2 and 3 in Fig. 2, in which a motif organization of their songs became apparent 8–10 days after onset of subsong. Bird 2 attempted early on a global imitation of its father's song, including the periods of sound and silence. The original sounds were noisy and imprecise, but they became more structured and stereotyped over a period of days and weeks. In this bird, each of the four syllables in the adult stable song could be traced back to four separate precursors delivered, as early as posthatching days 38–40, in a motif-like serial order, with silent intervals separating them. There were relatively few serial repetitions of any syllable in this bird at any point in song ontogeny.

The song development of bird 3 (Fig. 2) revealed another version of motif strategy. In this second motif strategy, all syllable precursors were initially delivered without the silent gaps that normally separate syllables in adult song. This manner of singing was already recognizable by posthatching day 40; at that time, the forerunners of four syllables (B–E) that eventually became a close match of the model's syllables were produced as an uninterrupted sound. Whereas the differences between the serial repetition strategy and the motif strategy are easily recognized at times when one or the other predominate, the differences between the two motif strategies described above for birds 2 and 3 are bridged by intermediate cases, where silent gaps between the different syllable precursors can be more or less obvious. The remarkable facts about the three birds in Fig. 2 are that they were siblings, they were members of the same clutch, and they all imitated the same model.

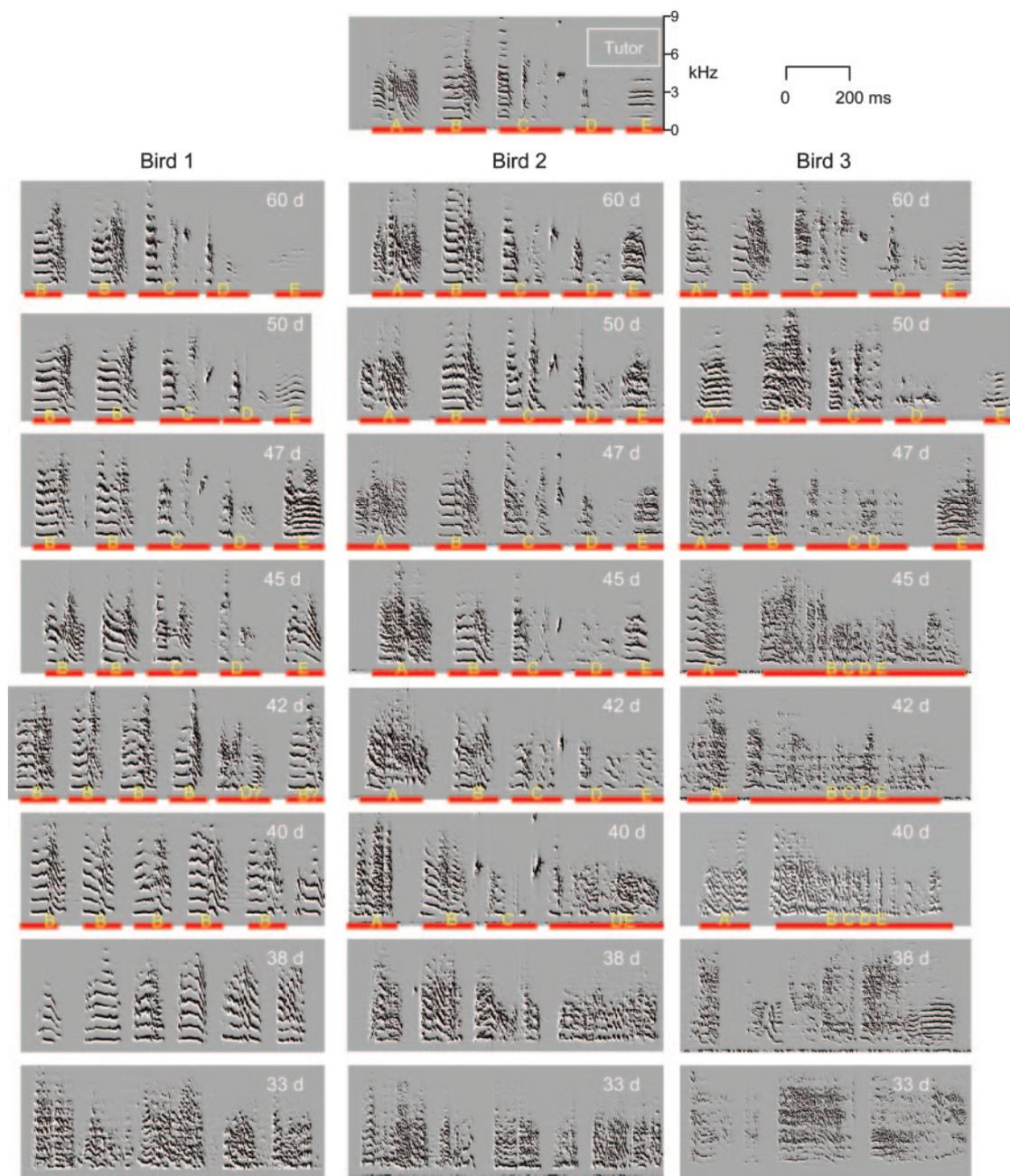


Fig. 2. The ontogeny of the song motif in three juvenile zebra finch siblings (birds 1, 2, and 3). The siblings were members of the same clutch and mastered the 1-s-long song motif of their father, labeled "Tutor" in the box on top. The vertical axis corresponds to frequency, in kilohertz, and the horizontal axis corresponds to time, in seconds. The highly stereotyped song motif of the father consisted of five different syllables, identified by letters A–E; each syllable is separated from the next one by a silent interval. In adult song, the motif is repeated several times, back to back, in a bout of song that lasts several seconds. Bouts of similar duration also occur in juveniles. The vocal ontogeny path that each sibling followed until it achieved a close imitation of the tutor song motif is shown by a selection of sounds recorded from the end of the first month after hatching (bottom panels) up to day 60. The examples shown were chosen visually, seeking for each day the best match with the tutor song motif. Further refinements in imitation, not shown here, continue to occur after day 60; by day 90 adult, stable song is in place (data not shown). All of the syllables (A–E) present at 60 days can be tracked to earlier instances, labeled likewise or, for the earliest or less similar versions, labeled A', B', etc., which were already in place by about 40 days. For more details, see *Results*.

We were concerned that the appearance of strategy differences based on visual inspection of sound-spectrographs might be influenced by our own perception of what the birds were doing, and so we resorted to a more objective, computer-aided analysis (see *Materials and Methods*) of song development in the same 15 clutches discussed above. In this more rigorous quantitative analysis, we examined the incidence of syllable repetition (Figs. 3*a* and 4) and the time course of song imitation (Fig. 3*b*).

For this more quantitative approach, we used only 23 birds; these birds came from clutches that had two to five males, and the song of each of them had, by posthatching day 60, a 70% or better similarity with the model song. We restricted the sample in this manner because we wanted males that had a similar time frame of song development, that were similarly successful at matching their model, and that had at least one other male sibling in their clutch. For a small subset of 6 birds, song samples were taken

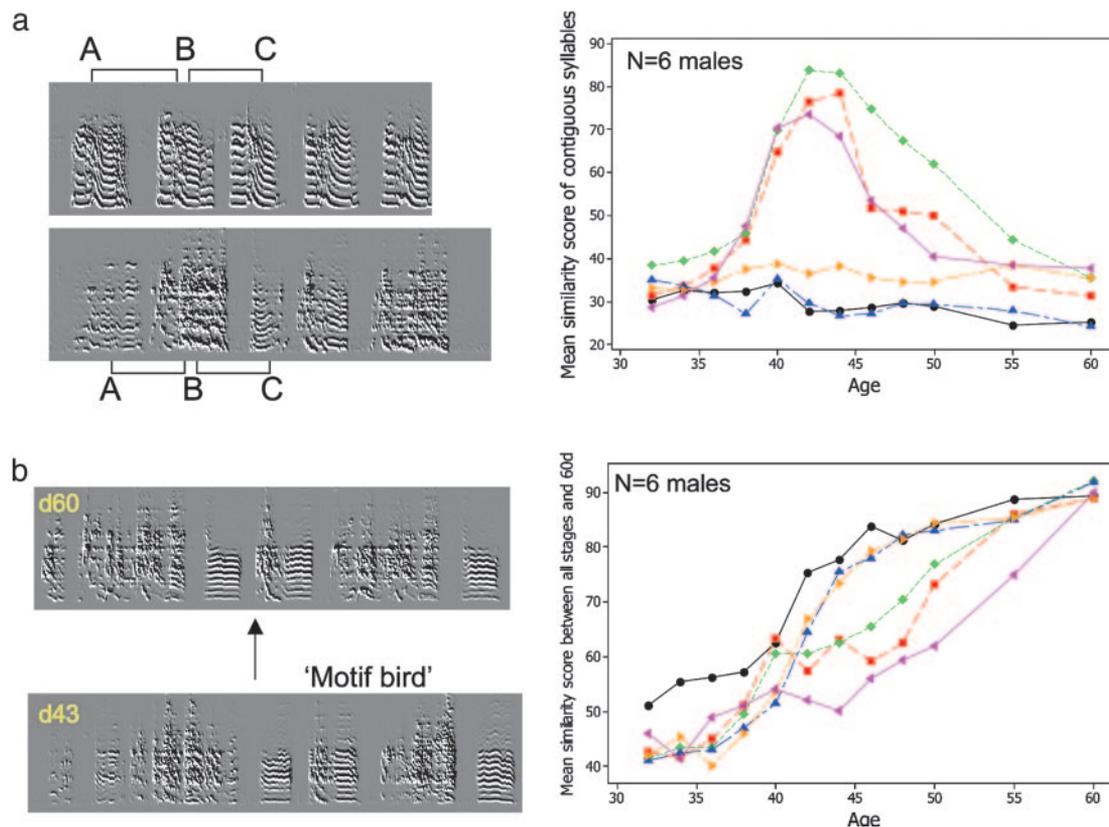


Fig. 3. Two approaches that quantified changes of song during the first 60 days. (a) The graph shows mean similarity scores for contiguous syllables recorded in a subset of 6 of our 23 birds that were followed from early subsong (day 32) until the birds produced a clearly recognizable approximation of the tutor song on day 60; three of the birds sang in the serial repetition manner (Left Upper) from day 40 to day 50; the other three sang during this same time in the motif manner (Left Lower). In both cases, for each song sample, syllable A is compared with B, B with C, and so on. (b) For the same six birds, we identified the song that on day 60 (Upper) came closest to the tutor song for that bird. Then we estimated the similarity index obtained when comparing that song and another song on each of several previous days, going back to day 32. The results for each day are based on a sample of 100 songs per bird. Notice that on day 45, three of the birds, representatives of the motif strategy, had higher similarity to the target song than the other three, which showed a high incidence of linear repetition (color identification as in a). In this case the two panels in Left emphasize the type of comparison, between earlier and later song that went into the graph.

every other day (Fig. 3a), but it was not possible to do this for all 23 birds, so song samples for them were taken at three times (32, 43, and 60 days after hatching; Fig. 4). We obtained for each

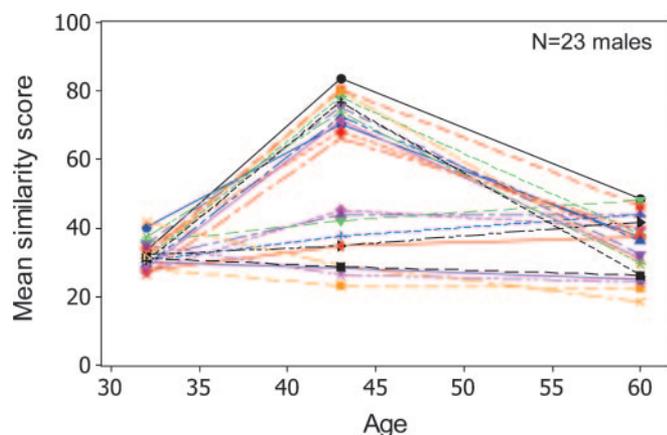


Fig. 4. Mean similarity score for contiguous syllables, as in Fig. 3, for the whole group of 23 birds; scores were obtained by using three recording times meant to characterize events during early subsong (day 32), early plastic song (day 43), and later plastic song (day 60). Note that on day 43 similarity scores clump into two separate clusters that correspond, respectively, to the serial repetition and motif strategies.

of these 23 birds, at each sampling time, a mean similarity score for contiguous sounds; these were sounds separated from the previous and subsequent ones by a silent interval of at least 20 ms. During subsong (posthatching day 32), the mean similarity between contiguous sounds tended to be, in all juveniles, low. During early plastic song (posthatching day 43), the range of similarity between contiguous sounds was much broader. In approximately half of all birds sampled, similarity scores remained at this stage as low as during subsong; in the other half, mean similarity scores were significantly higher than during subsong (Fig. 4). Inspection of the sound spectrographs of the song of birds in these two groups revealed, respectively, birds using predominantly the motif and serial repetition strategies. On the last sampling day (posthatching day 60), all birds had converged on a comparably sparse incidence of serial repetition, and their songs showed a close approximation to what would be the adult pattern, with the normal succession of different syllable types.

The results shown in Fig. 4 suggest that there is on day 43 a clear separation between individuals that follow predominantly a motif strategy and those that follow predominantly a serial repetition strategy of song ontogeny. Next, we wanted to determine the actual incidence of serial repetition during the three stages of song ontogeny described above; we focused on the same 23 birds described in the previous paragraph, and these results are presented in Fig. 5a. For this test we defined as serial repetition the occurrence of three contiguous sounds that

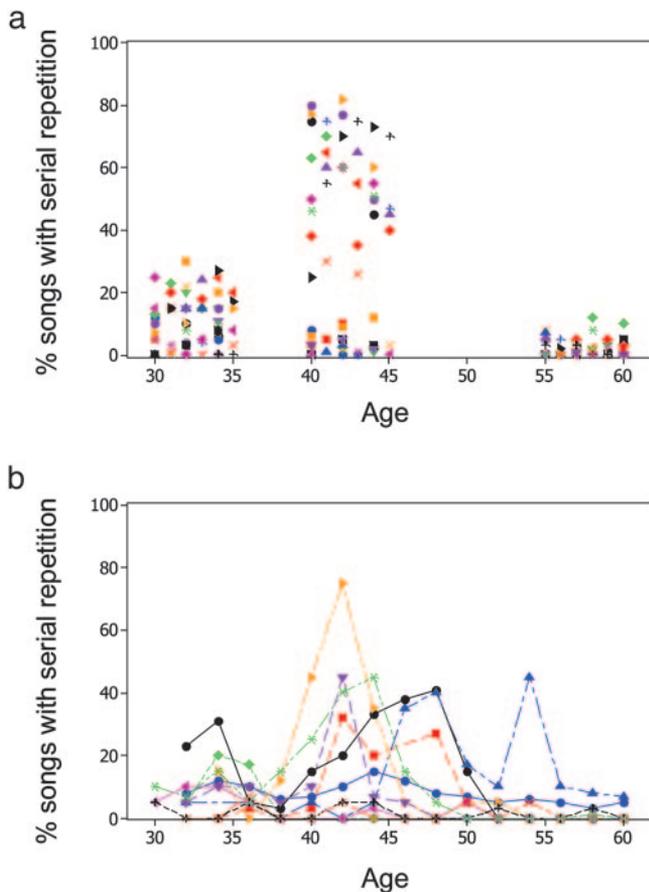


Fig. 5. Effects of social setting on the incidence of serial repetition. (a) Sound recordings made from 23 males kept with their families during the subsong (days 30–35), early plastic song (days 40–45), and later plastic song (days 55–60) stages; during those times, each bird was recorded every other day, and birds were recorded on the same day. (b) Sound recordings made every other day from day 30 until day 60 from 12 birds kept singly with an adult. The vertical axis indicates the percentage of all songs produced by a bird during those times that included three or more serial repetitions that met the criterion of 75% similarity.

showed at least 75% similarity. The range of serial repetition varied from 0% to 30% during the early subsong stage (30–35 days old), but it broadened during the next sampling period (40–45 days old). In one group of birds ($n = 10$), 40–80% of all songs included serial repetitions; these birds were “high repeaters.” In the other group ($n = 11$), the incidence was lower, 0–20% (Fig. 5a), and we shall refer to them as “low repeaters.” Two birds straddled the two groups. It was among birds in the low repeater group that we found our best examples of early motif organization, which, in turn was much less common among high repeaters. Subsequently, the performance of these two groups of birds converged, so that by days 55–60 the incidence of serial repetition was fairly low in all 23 birds.

In all 15 clutches sampled, members of the same clutch commonly used different strategies to master their imitation of the same tutor, as shown by the three siblings in Fig. 2. In all 15 clutches studied, at least one male sibling in each clutch used predominantly the motif strategy ($n = 18$), and one used predominantly the repetition strategy ($n = 16$). In our 15-clutch sample, the first sibling to start singing adopted a motif strategy in five cases and a serial repetition strategy in seven cases. (For three other clutches, we were unsure which bird was the earliest singer.) It appears that male zebra finches learning their songs

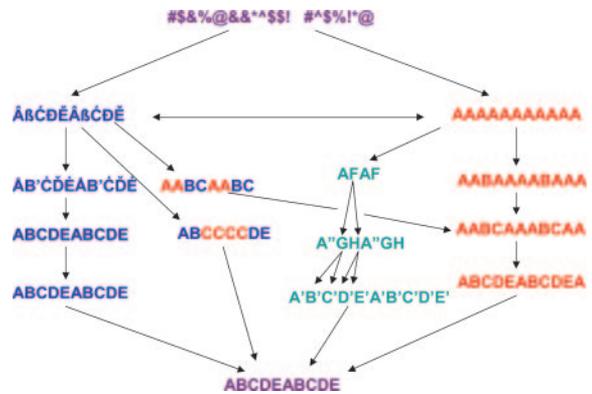


Fig. 6. A diversity of trajectories can lead to the same end. The top line is meant to show the poorly structured and diverse sounds of subsong. During plastic song, some birds follow from early on a motif trajectory (left), others a serial repetition trajectory (right); they can go back and forth between these two, but usually one or the other trajectory is emphasized. There are potential branching points. Toward the end of the process, all these trajectories converge on the same final output.

avoid the strategy of the sibling whose song is closest in developmental stage.

Interestingly, juveniles favoring the serial repetition or the motif strategies were able to acquire a comparably accurate imitation of the model song. When a clutch included more than two males, not every juvenile produced a good imitation (11). The male sibling that produced, in each clutch, the best imitation (>90% similarity with the model song) used during the 35- to 50-day period either a low-repetition ($n = 7$) or high-repetition ($n = 8$) strategy to develop its song, suggesting that both approaches are similarly effective for mastering an imitation.

Social Influence on Learning Strategy. We speculated that juveniles within the same clutch use different song development strategies to mitigate the inhibitory effect of another sibling’s song on the process of model imitation (11). We tested this idea by removing 12 juveniles aged 20–25 days from their mothers and siblings, housing each of them in a separate sound-proof chamber with an adult male zebra finch, and recording how each juvenile developed its song. Eleven of the 12 males produced, eventually, a good imitation of the adult model (similarity score of >75%), but they did not use the same strategy. Four juveniles used during the 40- to 45-day period a pure motif (low repetition) strategy; one bird used a high repetition strategy and did not sing in the motif manner during the 40- to 45-day period. The remaining seven produced during that time a fair approximation of the entire motif that they would sing at 90 days while showing, at the same time, a frequent occurrence of serial repetitions; so theirs was a “mixed” strategy. Moreover, whereas only 1 bird out of the 11 included three or more contiguous repetitions in >50% of all songs produced during the 40- to 45-day period (Fig. 5b), 10 birds out of 23 met this criterion in the family-reared group (Fig. 5a), and this difference was significant (Fisher’s exact test, $P < 0.01$). We infer from this comparison that, whereas singly reared juvenile zebra finches can develop their imitations of a song model by using either the repetition or motif strategies or a mixture of both, options that therefore are probably available to all juvenile males, a greater polarization of developmental trajectories occurs when siblings exposed to a single model grow up together. It is possible that in nature, where juvenile zebra finches are normally exposed to a variety of models that they can copy (7), this polarization is not as great as it is in single-family settings.

The similar effectiveness of high repetition and low repetition

strategies in song development can be tested in still another way. Fig. 3*b* shows that low repeaters (i.e., motif strategy birds) and high repeaters start from a common level of song imitation at day 32. After this the low repeaters approach the model faster, yet by day 60, the difference between the two groups has disappeared. Because zebra finch males do not breed before age 70–80 days, at the earliest (6), our conclusion stands that both strategies of song imitation should be equally serviceable to the birds that use them.

Discussion

An earlier study (4) suggested that song imitation in zebra finches commonly started with successive repetitions of a same precursor syllable. In that study, each juvenile was raised singly by its mother until it was 30 days old and then housed singly in a sound-proof chamber, without any access to a social tutor or tutor song until 43 days of age, when this juvenile was allowed to peck at a key that resulted in song playback (each time the same song, identically repeated) emanating from the chest of a plastic adult male model. In the present study, the variety of strategies available for song learning became apparent, particularly in the juvenile males that were raised and acquired song in a family setting, which is the natural social environment for juveniles. It is possible that a variety of trajectories for achieving song imitation are always part of vocal learning and that it is only under conditions of severe social deprivation, invariant repetition of the playback signal, and/or delayed exposure to a model that less diverse trajectories are encountered.

Although we have emphasized two different ways of imitating a model, one with many repetitions of an early syllable and one providing a coarse approximation to the whole motif, there are also cases in which birds seem to use both ways, at times singing in the motif manner and at other times repeating many times the same syllable. In addition, even repetition might be used to more than one end, for example, to rehearse a single syllable (figure 1 in ref. 4) or to give rise to multiple syllables (figure 5 in ref. 4 and this report). Moreover, the route followed by any one bird can move from one strategy to the other and even explore variants on which we have not dwelled (Fig. 6). For this reason, it is probably best to say, quite simply, that song can be imitated in several different ways.

Zebra finches and other estrildid finches are special in that song learning occurs while juveniles are still close to other family members. These birds may encounter, from the time they fledge until they reach independence at ≈ 40 days, a greater variety of social circumstances than other less colonial and gregarious songbirds. For this reason, the variety of vocal learning styles found in zebra finches need not apply to all oscine songbirds. Interestingly, although, social variables affect vocal learning even in less social oscine song birds (12). Moreover, the variety of strategies may have evolved not only to cope with variable social

settings, but to enable a young bird to imitate either a whole song or just parts thereof, or even, in the case of the high repeaters, provide a means for not committing prematurely to a particular song model. Because the many syllables of a song occur, from their earliest expression, in the order in which they will appear in the adult song, syllable repetition can be thought of as a way of holding “slots” for syllables that have not yet been acquired, thereby extending the time during which a juvenile bird can acquire song material by imitation. In sum, the variety of strategies for vocal imitation found in zebra finches may be the norm rather than the exception. Although it had been reported before that social bonds play an important role in vocal learning, we are surprised that this interaction starts so early in vocal ontogeny and that it involves not only the bond with an adult but also relations among siblings.

As in zebra finch juveniles, infants too show remarkable variability in the way in which they achieve eventual mastery of the sounds of language. Whereas some infants focus, at the onset, on serial repetitions of a same word, others go through a stage where they use fairly imprecise short phrases for which, eventually, the words become clearer. The manner of speech of the latter children has been compared with the cadence, in terms of inflexion and emphasis, of the adult phrase, although it still lacks recognizable individual words. These two strategies are very different, and children often use both in a way that cannot be related to the parents’ efforts to guide speech development (13–16). Thus, in both infants and zebra finches, vocal learning does not unfold in a preset manner but rather emerges as an exercise in problem solving that leaves much room for external influences and individual learning styles. Overall, our observations add in unexpected ways to the many known similarities between vocal learning in birds and humans (17, 18). As in the past, we are struck by the fact that songbirds, with brains 1,000 times smaller than those of humans and with a very different evolutionary history, go about vocal learning, nonetheless, in ways that are not all that different from ours.

We would like to end with a question. Did the multiple ways to learn sounds evolve to meet the special needs of vocal learning or do they reflect a general ability of advanced brains to master skills in a variety of ways?

We thank Drs. Peter Marler, Ofer Tchernichovski, and David Vicario for reading an earlier version of the text and offering many useful comments. In addition, Dr. Tchernichovski provided invaluable advice with use of the SOUND ANALYSIS software that we used for analyzing our zebra finch song recordings. We also thank Daun Jackson, Sharon Sepe, and Helen Ecklund for their expert care of our birds. This research was conducted with the support of Public Health Services Grant MH18343, and W.-c.L. was supported by a Li Memorial Scholar Fund fellowship. This work was made possible, too, by the generous support of the Mary Flagler Cary Charitable Foundation, the Herbert and Nell Singer Foundation, and the Phipps Family Foundation.

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