A preference for own-subspecies' song guides vocal learning in a song bird

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In many song birds, males develop their songs as adults by imitating the songs of one or more tutors, memorized previously during a sensitive phase early in life. Previous work using two assays, the production of imitations by adult males and playback-induced calling by young birds during the sensitive phase for memorization, has shown that song birds can discriminate between their own and other species' songs. Herein I use both assays to show that male mountain white-crowned sparrows, *Zonotrichia leucophrys oriantha*, must learn to sing but have a genetic predisposition to memorize and learn the songs of their own subspecies. Playback tests to young naive birds before they even begin to sing reveal that birds give begging calls more in response to *oriantha* song than to songs of another species. After 10 days of tutoring with songs of either their own or another subspecies, birds continue to give stronger call responses to songs of their own subspecies, irrespective of whether they were tutored with them, and are more discriminating in distinguishing between different dialects of their own subspecies. The memory processes that facilitate recognition and discrimination of own-subspecies' song may also mediate the preferential imitation of song of a bird's own subspecies. Such perceptual biases could constrain the direction and rate of cultural evolution of learned songs.

The success and persistence over time of culturally transmitted behavior patterns likely reflects the joint operation of natural selection and cultural selection (1–3). Cultural selection, the differential transmission of learned variants, may result in part from learning preferences that individuals exhibit for certain behaviors. If such learning preferences were molded by natural selection, we would expect to find genetically based predispositions to learn certain stimuli more readily than others.

Bird song provides one system in which to study cultural evolution. Young males model their songs on those of older males and, in the absence of exposure to such songs, produce simple "isolate" songs (4, 5). Males of several species also exhibit a preference to learn their own species' song when given a choice (6–8). As a consequence of learning, males of many species form local "dialects" in which neighboring males sing similar songs that differ from those of males at other localities (9, 10). Such dialects, passed from one generation of males to the next, may persist for decades and thus qualify as cultural traditions (11–14).

Song learning occurs in a two-stage process. In the first stage, songs are committed to memory during a sensitive phase, which is often restricted to the first few months of life (15, 16). In the second stage, termed the sensorimotor stage, the stored memory trace, or template, guides motor development of the bird's own song via auditory feedback (5). In the sparrow species that exhibit learning preferences, the sensorimotor phase may follow the sensitive phase by several months. Studies demonstrating preferential song learning have used the standard technique of comparing the songs developed by young males to those of their tutors. The species selectivity of learning revealed by this technique could possibly be the consequence of anatomical and neural constraints on the production of imitations and need not necessarily reflect perceptual (memorization) preferences (17). Herein I use a song playback technique to compare the responses of very young birds to tutor songs and novel songs during the sensitive phase for song memorization before production of any imitations (18, 19). I develop several measures of preferential memorization based on responses made during the sensitive phase and compare these measures to the standard measure of preferential learning based on imitations produced many months later.

Song playback to young birds has established two results to date. (*i*) Before experience with tutors, newly fledged white-crowned sparrows give significantly more begging calls or "chirps" to playback of conspecific song than they do to heterospecific song (18, 20). (*ii*) After tutoring with conspecific models for 10 days, young males and females give more chirps to playback of tutor songs than to novel songs. This differential responsiveness only occurs during the early sensitive phase for song memorization, as independently defined by monitoring the production of imitations of tutor songs by adult birds (19).

Only species-level song learning preferences have been demonstrated in birds so far, and it is unknown whether males have more subtle preferences (e.g., between subspecies or dialects) in choosing songs for learning (21). One goal of this experiment was to explore whether males of the mountain white-crowned sparrow, *Zonotrichia leucophrys oriantha* (hereafter *oriantha*), living in the California Sierra Nevada, exhibit a learning preference for dialects of their own subspecies over those of Nuttall's white-crowned sparrow, *Zonotrichia leucophrys nuttalli* (hereafter *nuttalli*) living on the coast some 200 km away (22) (Fig. 1). The second goal was to use the song playback technique to identify when and how any such preference develops during ontogeny.

Methods

General Experimental Plan. Chirp responses to song playbacks were measured in hand-reared, recently fledged birds (test 1) and in the same individuals after 10 days of experience with tutor songs (test 2) (Fig. 1). The aims were to compare initial responsiveness to songs of both subspecies and to determine how well birds discriminate between dialects of their own subspecies and the other subspecies. Thus, each test had two parts, a recognition trial, measuring the stimulus selectivity of the evoked calling response (18, 20), and a discrimination trial, in which the ability to notice differences between two stimuli was measured after habituation to one of them, a method inspired by research on speech perception by human infants (e.g., see ref. 23). In test 2, after tutoring, I sought to determine how tutor experience affected the birds' ability to recognize and discriminate different dialects of their own species' song.

In the recognition trial, 10 repetitions of one dialect were presented at 10-sec intervals and calling was monitored. In the discrimination trial, which followed immediately, the same dia-

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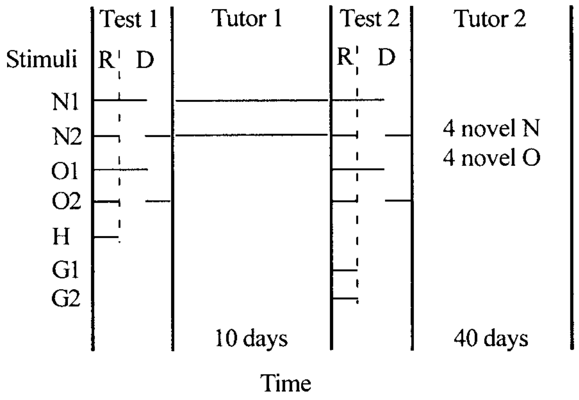

Fig. 1. Diagram of the experimental plan for one subject. Horizontal lines depict stimuli presented during tests 1 and 2 and during tutoring. N, *nuttalli* dialect; O, *oriantha* dialect; H, heterospecific song; G, generalization song, in this case two novel *nuttalli* dialects. A few days after fledging, the bird heard playback of five stimuli in recognition (R) trials and two pairs of habituation/dishabituation stimuli in discrimination (D) trials (for examples of stimuli and text for description of protocol, see Fig. 2). This bird was then tutored for 10 days with the two *nuttalli* stimuli, and then the recognition and discrimination trials were repeated in test 2. No heterospecific song was presented in test 2; instead, two generalization stimuli were presented. After test 2, all birds were tutored with the same eight novel dialects for 40 days. The time axis is not to scale; for a given bird tests 1 and 2 took place on a single day.

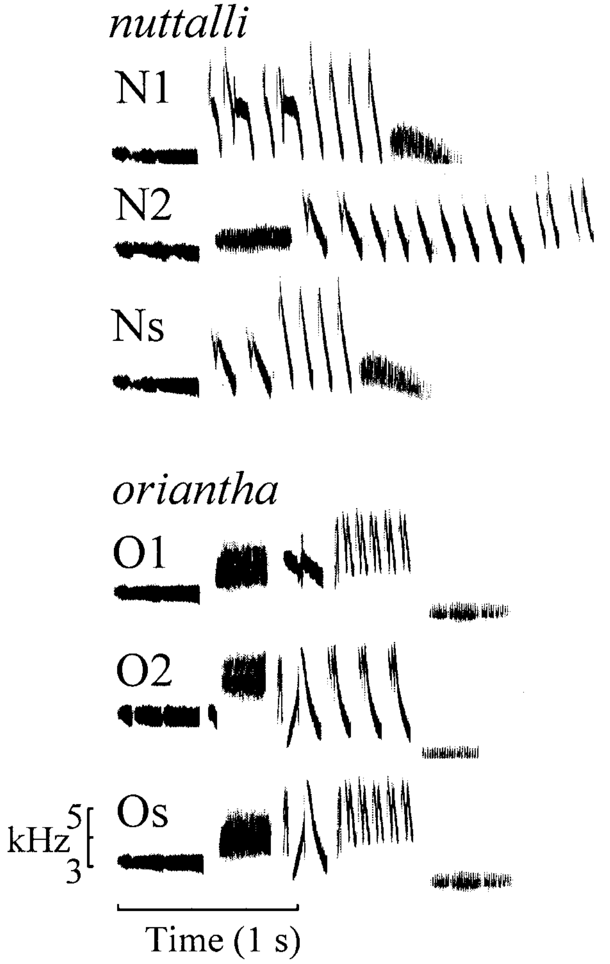

Fig. 2. Sound spectrograms of some of the *oriantha* and *nuttalli* songs used as stimuli. In discrimination trials, *nuttalli* dialect N1 (for example) was used as a habituation stimulus, and either *nuttalli* dialect N2 or Ns was the dishabituation stimulus. Ns was a synthetic hybrid song created by replacing the complex syllables of N1 with those of N2. N1, N2, *oriantha* dialect O1, and O2 were used as habituation stimuli in both tests 1 and 2, and different versions of Ns and Os were synthesized depending on which song was used as the habituation stimulus. Ten pairs of natural *nuttalli* and *oriantha* dialects were used for different birds.

lect was presented at 10-sec intervals until the calling response declined to at least one-half the initial rate. A dishabituation stimulus then was presented, either the same song again or a different dialect. The extent of response revival provided an index of the discriminability of the prehabituation and posthabituation stimuli. In test 1, the recognition stimulus set consisted of two dialects of the same subspecies, two dialects of a different white-crowned sparrow subspecies, and one song of another species. Between tests 1 and 2, each bird was tutored for 10 days with two dialects of one or the other subspecies. The same two "tutor" dialects and two dialects of the other subspecies were used as stimuli for a given individual in tests 1 and 2. In addition, in test 2, two additional novel dialects of the same subspecies as the tutor stimuli were used (Fig. 1) as generalization stimuli to determine whether any learning that took place during tutoring was generalized to other dialects of the same subspecies as the tutors.

Subjects. Nestling mountain white-crowned sparrows of both sexes (16 males and 12 females) were collected in 1995 between the ages of 4 and 7 days and hand-reared to independence at 21–28 days of age by using established methods (22). It is unlikely that the subjects learned song while in the nest in the wild because there is good evidence that altricial song birds begin to learn song only after they leave the nest (24, 25). Playback test 1 began at the age of 11–13 days, 2–3 days after fledging. On the day before and during testing, subjects were individually housed in sound isolation chambers.

Test Stimuli and Tutor Stimuli: Test 1. The five stimuli (two *oriantha* dialects, two *nuttalli* dialects, and one heterospecific song) were presented once in random order at 1-h intervals. Stimuli were chosen from a catalog of 20 acoustically distinct conspecific songs sampled from different geographic dialects of the *nuttalli* and *oriantha* subspecies (22). Each bird was randomly assigned one pair of dialects of each subspecies (Fig. 2). Ten songs from four other species that breed at the collection site were used as heterospecific controls. Stimulus presentation was controlled by computer (26). Amplitudes were normalized at 76 dB in the center of the chamber.

Recognition Trial. After a 100-sec preplayback period, subjects heard 10 repetitions (one repetition every 10 sec) of one of the five stimuli. The number of chirp calls were counted by a "blind" assistant during both the preplayback and playback periods either by ear or by using a real-time spectrograph program (19, 26). The calling rate was adjusted by subtracting the number of calls in the preplayback period from the number in the playback period.

Discrimination Trial. In the discrimination trial the stimulus used in the preceding recognition trial was presented immediately and repeatedly at 10-sec intervals until the calling response decreased to at least one-half the initial rate. On reaching this criterion, a control trial was performed by disconnecting and reconnecting the speaker cable in the quiet interval between songs and then playing five more habituation stimuli. The speaker cable was then disconnected and connected to the

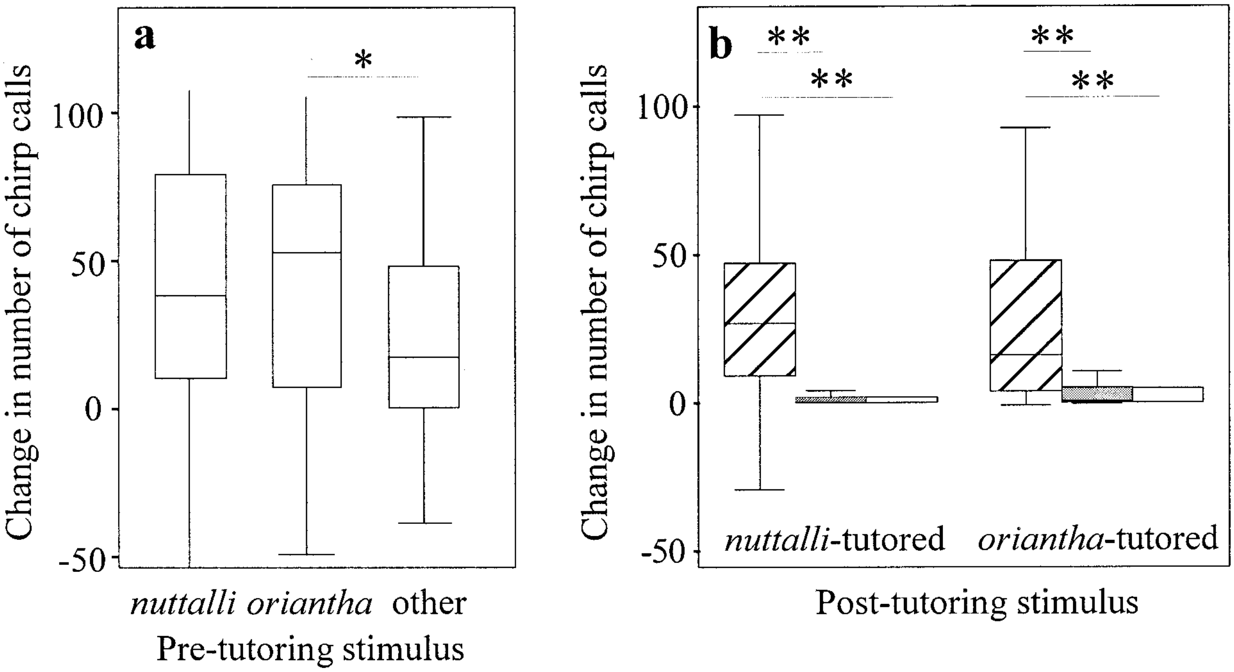

Fig. 3. (*a*) Change in call rate in response to song playback of own subspecies (*oriantha*), *nuttalli*, and heterospecific songs before tutoring (test 1, $n = 28$ birds in all three groups). (*b*) Call rate change in response to tutor song (cross-hatched bars), novel song (shaded bars), and generalization song (open bars) after tutoring with either *nuttalli* or *oriantha* songs (test 2, $n = 11$ in both groups, six nonresponders). After tutoring birds call more to the tutor song. Tests are Wilcoxon matched-pairs signed ranks comparing the groups linked by horizontal lines. *, $P < 0.02$; **, $P < 0.01$. The lower and upper edges of the boxes represent the first and third quartiles; the median bisects each box. The vertical lines include the range of values within 1.5 times the interquartile range.

second channel of the playback computer that played the dishabituation stimulus: this was (*i*) a different dialect of the same subspecies as the habituation stimulus or (*ii*) a synthetic hybrid song created by electronically substituting some of the syllables from a different dialect of the same subspecies into the habituation stimulus (Fig. 2). Equal numbers of natural and synthetic songs were used as dishabituation stimuli. Each bird received two habituation trials (conducted after two of the five recognition trials), one with one of the two *nuttalli* dialects and one with one of the two *oriantha* dialects used as its recognition stimuli. Habituation stimuli were chosen at random.

Tutor Block 1. After test 1, birds were randomly assigned to two treatment groups: half were tutored daily for 10 days with the pair of *nuttalli* dialects they heard in test 1 and half with the pair of *oriantha* dialects. One-hour tutor sessions were conducted in the morning and midafternoon. Each session contained 72 repetitions of one dialect (six songs per min), 5 min of silence, and then 72 repetitions of the other dialect. Birds were housed in sound boxes in pairs or trios for tutoring but were housed individually in test 2.

Test 2. After 10 days of tutoring, birds were tested again with playback of the same two tutor dialects and the other two conspecific dialects they heard in test 1 but did not hear during tutoring (novel songs). Note that the novel songs were of a different subspecies from the tutor songs. Each bird also was tested for recognition only of two novel dialects of the same subspecies as their tutor songs (generalization songs; Fig. 1). Mean responses to tutor, generalization, and novel songs were calculated per bird. Discrimination trials were run after the recognition trials of one *nuttalli* and one *oriantha* dialect, the same dialects as used for each bird in test 1.

Tutor Block 2. In tutor block 1, individuals heard two dialects of one of the subspecies. To give them a choice of both subspecies songs as learning stimuli, males were tutored for an additional 40 days beginning the day after test 2 when birds were between 23 and 25 days old. The tutor tape contained eight novel dialects (four *nuttalli* and four *oriantha*), presented twice daily. Each dialect was repeated 18 times (six times per min), with 40 sec of silence between different types on one side of the tape. The second side contained the same eight types presented in a different, randomly determined, order. The entire tape was played twice a day.

Song Analysis. Singing was recorded weekly beginning when males were 210 days old and continuing until songs were crystallized. To stimulate singing, birds were tutored during this period with two novel dialects in the morning and afternoon. These songs were not imitated by any bird. Sonagrams of tutor imitations present in plastic song, the stage of practice singing before crystallization of the single adult song, were matched by eye by two observers to sonagrams of the 10 tutor songs that each male heard. The proportion of *oriantha* songs in each subject's repertoire was compared with the proportion expected to be learned by chance. Nonparametric tests were used because the data did not meet distributional assumptions of parametric tests. Sample sizes in all tests are the number of birds and vary because some birds did not respond in both playback tests or did not habituate after playback.

Results

In test 1 recognition trials, naive birds gave significantly stronger responses to white-crowned sparrow songs of their own subspecies (*oriantha)* than they did to songs of a different species ($P < 0.01$; Fig. 3*a*) before any tutoring. Responses to *nuttalli* songs were intermediate: they did not differ from responses to other species' songs ($P > 0.05$) or *oriantha* songs ($P > 0.05$). The average response to conspecific songs was significantly higher than the response to other species' songs ($P = 0.01$).

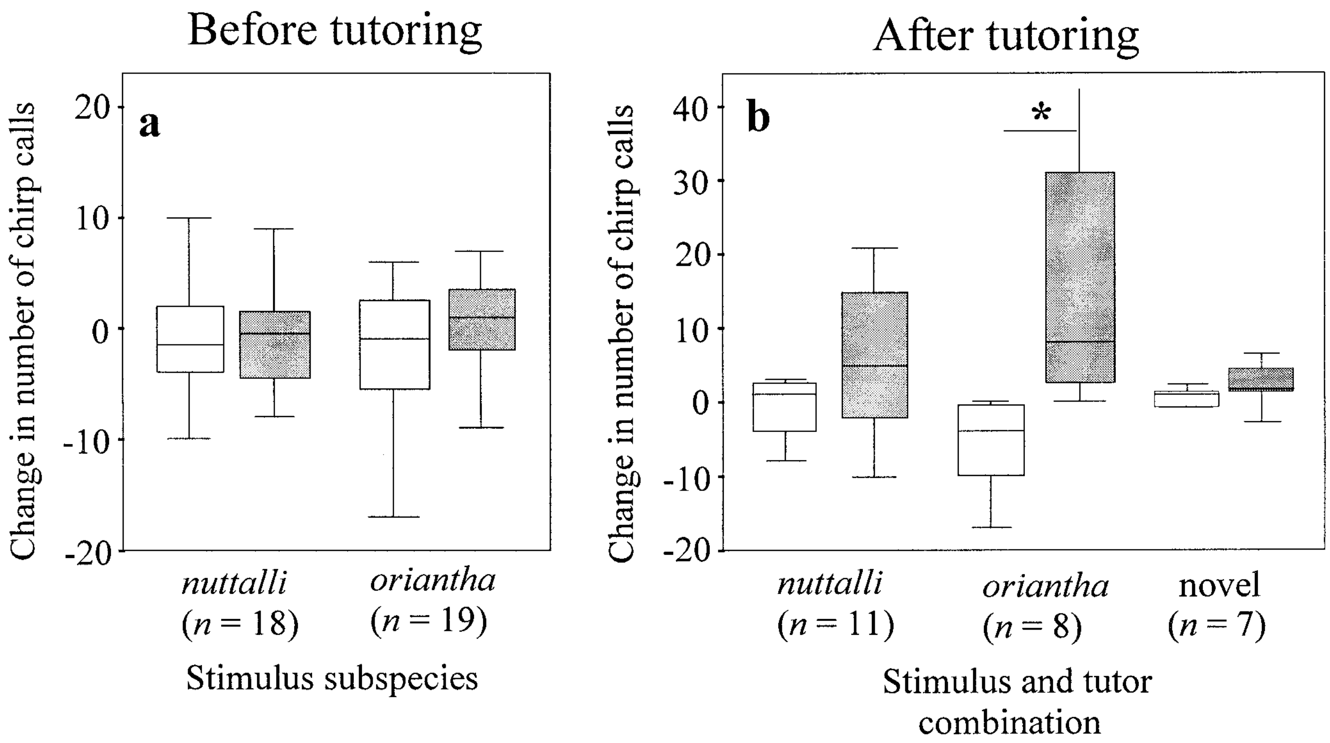

Fig. 4. Results of habituation-dishabituation trials before tutoring, test 1 (*a*), and after tutoring, test 2 (*b*). Open boxes (control trials), the call rate change with the same song as a dishabituation stimulus; shaded boxes (test trials), the call rate change after playback of a different dialect of the same subspecies as the tutor. Thus, birds are more discriminating after being tutored with same subspecies song. In test 2 (*b*), the categories refer to the combination of tutor and habituation stimuli (*nuttalli,* tutored and habituated with *nuttalli* songs; *oriantha,* tutored and tested with *oriantha* songs; novel, tested with the subspecies other than the tutor subspecies). In test 1, birds were played a median of 20 songs before reaching the habituation criterion and, in test 2, birds were played a median of 15 songs. *, $P < 0.02$, Wilcoxon matched-pairs signed ranks tests.

Next, in the discrimination trial of test 1, before any tutoring, subjects were habituated with the dialects used in the recognition test. Whether habituated with a *nuttalli* or an *oriantha* dialect, responses did not revive significantly more than in control trials when a new dialect of the same subspecies was substituted (Fig. 4*a*). Thus, before tutoring, subjects did not discriminate between different dialects of either subspecies.

After 10 days of tutoring with either *nuttalli* or *oriantha* dialects, test 2 recognition trials were conducted, and subjects gave significantly more chirps to songs they were tutored with than they did to novel songs (Fig. 3*b*). There were two indications of heightened responsiveness to own-subspecies (*oriantha*) dialects. First, in within-bird comparisons, responses to *oriantha* dialects declined less between test 1 and test 2 than did responses to *nuttalli* dialects, both when the songs were novel (Mann-Whitney $U = 26.5, n = 22, P = 0.02$) and after tutoring with them ($U = 27.5$, $n = 22$, $P = 0.03$). This is consistent with the hypothesis that own-subspecies songs are established or retained in memory more firmly than are the songs of another subspecies, whether or not there has been any tutoring with them.

Secondly, 10 days of experience with specific tutor stimuli changed the readiness to discriminate between the prehabituation and posthabituation tutor-song dialects; but this effect was obtained only with own-subspecies song tutoring. Birds tutored with *nuttalli* songs did not increase their call rate when the *nuttalli* dishabituation stimulus was presented in test 2 ($P = 0.2$; Fig. 4*b Left*). Those tutored with own-subspecies songs, however, increased their call rate significantly when the *oriantha* dishabituation stimulus was presented ($P = 0.~02$; Fig. 4*b Middle*), indicating discrimination between prehabituation and posthabituation dialects. In control trials, responses did not increase significantly for either group. In test 2, only seven birds called enough in response to other-subspecies songs [*nuttalli* stimulus after tutoring with *oriantha* (four birds) or *oriantha* stimulus after tutoring with *nuttalli* (three birds)] for the response to habituate. In discrimination tests with these seven birds, responses did not revive when a second song of the nontutor subspecies was played (Fig. 4*b Right*).

After memorization of tutor songs had occurred, generalization stimuli of both subspecies elicited significantly weaker responses than tutor songs, which were not significantly different from novel songs (Fig. 3*b*). Thus, tutored subjects did not generalize from having learned either *oriantha* or *nuttalli* tutor dialects to other dialects of the same subspecies. Evidently, learning that results from tutor experience is specific to a particular dialect.

After completion of test 2, birds were tutored for another 40 days with a second tutoring block ending about 60 days of age. Males did not begin to practice singing until the next spring, at approximately 215 days of age. During plastic song they produced imitations of a median of one tutor song (range = 0–2) from tutor block 1 and three tutor songs (range = 0–5) from tutor block 2. Males were equally likely to imitate either subspecies' song presented in block 1 when they were given no choice (Fisher's exact test, $n = 16$ males, $P = 0.12$). However, when given a choice of tutors, as they were in block 2, these males preferentially imitated *oriantha* tutor songs (Wilcoxon $Z = 2.13$, $n = 16, P = 0.033$). Of the tutors imitated in block 2, 67% were *oriantha* tutors, compared with 50% expected by chance.

Discussion

Young male mountain white-crowned sparrows preferentially imitated tutor songs of their own subspecies when given a choice during the sensitive phase for song memorization. Perceptual experiments conducted during the sensitive phase before any imitation provided independent evidence that these birds are able to recognize songs of their own species and subspecies. This enhanced readiness to attend to or encode songs of a bird's own subspecies during the sensitive phase presumably underlies the males' preferential production of such songs the next spring. This is so, even though they are proved to be capable of memorizing and producing both subspecies' songs.

Sensitive-phase learning can be characterized neurobiologically as an "experience-expectant" process in which representations are overproduced followed by selective retention, stabilization, and attrition as a function of sensory experience (27). A specific version of an experience-expectant process is Marler's neuroselective model of song learning (17, 28, 29), which assumes that the species' entire natural repertoire of song components is preencoded in the brain as a set of templates that guide memorization and subsequent production of imitations. Learning consists of selecting a subset of templates as a function of experience and then encoding them in particular sequential patterns, as instructed during tutoring. Such experience-expectant processing of sound could explain the very rapid and accurate memorization of species-typical sounds, which are a common and important component of the young bird's auditory environment. The current results are compatible with the hypothesis that the template structure may be sufficiently precise to encode acoustic differences in the songs of different subspecies. These templates may be "latent" (28) in the sense that they require specific sensory experience to activate them. Once activated, they may enable the improved discrimination of different dialects of the same subspecies, that I have demonstrated, and also facilitate memorization of those dialects for reproduction the next spring.

The results of the perceptual experiments suggest that the young birds' ability to distinguish between the songs of different species and their ability to discriminate between dialects of their own subspecies develop at different times and/or by different mechanisms. Naive birds clearly discriminated between conspecific and heterospecific songs, a result also found in two previous studies using this technique (18, 20). The birds must have a genetic predisposition to focus their attention on the appropriate species models for learning. A nonsignificant tendency to favor responding to own-subspecies (*oriantha*) songs was also apparent in naive birds. But it was only after 10 days of tutoring that two clear indications emerged that *oriantha* dialects hold a privileged status in memory: responses to *oriantha* dialects decreased less than responses to *nuttalli* dialects between tests 1 and 2, irrespective of which type was used as a bird's tutor songs; also *oriantha* songs were discriminated better by *oriantha*-tutored birds than *nuttalli* dialects were discriminated by *nuttalli*-tutored birds in test 2. Both results suggest that songs of the birds' own subspecies are processed differently than other songs.

The discrimination trials clearly revealed that birds required tutor experience with particular dialects before they were able to discriminate them. Apparently the representation of song that naive birds possess (test 1) is sufficiently detailed to allow them to recognize conspecific songs and, possibly, to recognize consubspecific songs but does not encode the details of particular dialects. The representations formed during tutoring are highly dialect-specific: birds did not generalize their responses to other dialects of the same subspecies they were tutored with. Stimulus specificity in song learning is also demonstrated by the well-known ability of young birds to faithfully reproduce the idiosyncracies of their tutors' songs (30–32). This learning results in changes in the brain centers involved in song production and perception (33, 34) and affects behavioral responses as well (35–37). Thus the prerepresentations or templates that focus the naive bird's attention on conspecific and consubspecific songs appear to be modified by experience to encode the details of particular tutor songs. Experience has both a selective effect on song development, by activating specific templates, and an instructive effect, by modifying those templates (7, 21).

Aside from mimics such as starlings, *Sturnus vulgaris*, and northern mockingbirds, *Mimus polyglottos*, learning of heterospecific song is rare in nature but can be induced in the laboratory under certain conditions. Heterospecific song acquisition might occur by a different, general, experience-dependent process (27). This process may not involve the template system or may invoke templates only if heterospecfic song resembles conspecific song to some degree. In fact, there is evidence that birds are more likely to learn heterospecific songs if these resemble their own species' song (38, 39). Learning heterospecific song is more difficult for white-crowned sparrows than learning conspecific song: learning the former requires a live tutor or a hundredfold increase in the frequency of taped tutoring relative to conspecific song (40, 41). Heterospecific imitations are also usually not as complete as conspecific imitations (7, 38, 40). The relative difficulty of learning heterospecific song supports the hypothesis that the mechanisms involved differ in degree or kind from those involved in learning conspecific song.

Bird song is an important behavior that influences male mating success and, therefore, is subject to sexual selection (42). The role of neural or sensory biases in sexual selection of male traits has received much attention recently from evolutionary biologists because such biases could influence the way in which male sexual signals evolve (43, 44). Female song birds also memorize song, and other evidence indicates that songs memorized by females during the sensitive phase are retained and responded to sexually as adults (45). It seems likely that common perceptual mechanisms underlie the learning of song for production in males and the learned preference for song in females (46). It is now clear that these perceptual mechanisms include genetic predispositions to learn the songs of a bird's own species (6, 8) and subspecies. Such learning preferences for song in male and female birds could influence the direction and rate of cultural evolution of song (1–3).

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