S01-4　Social aspects of song learning and repertoire use in birds

Dietmar TODT[1], Henrike HULTSCH[2]

Institute of Biology, Free University of Berlin, Haderslebener Str. 9, 12163 Berlin, Germany; [1] todt@zedat.fu-berlin.de,
[2] hultsch@zedat.fu-berlin.de

Abstract　Two results from song tutoring experiments with nightingales (*Luscinia megarhynchos*) are presented: song learning by males, and the behavior of females tutored with conspecific master songs as young birds and again as adults. In these learning experiments, human individuals who cared for the birds served as social tutors, controlling for differences in social or experimental variables. The study supplemented results from our earlier work with four findings: 1) when exposed to tutoring regimes that simulated vocal interactions between two different tutors, one familiar and one unfamiliar, male subjects learned well from either tutor; 2) males, however, performed songs imitated from the unfamiliar tutor more frequently than songs imitated from a familiar tutor; 3) either type of imitation was always delivered with those derived from the same social origin, familiar or unfamiliar tutor; and 4) females did not develop any song-like vocalization. In order to determine if they learned and remembered cues from the earlier tutoring programs, we exposed these females to an additional playback of nightingale song. Results were equivocal as their behavioral responses did not allow us to determine if females discriminated between tutored and novel songs. Rather, adult females approached loudspeakers presenting "whistle-songs" (details in Metz and Todt, in prep.). In conclusion, our results point to strategies of song learning and use that appear flexible in either sex and which in males reflect an adaptation for using large repertoires of different songs as well.

Key words　Social factors, Song learning, Repertoire use, Gender-related differences, Nightingale

1　Introduction

In most oscines, song learning is gender-related and mainly limited to young males (Baptista, 1996). Usually, such males are affected strongly by the social properties of their environment, i.e. they acquire their songs from a live tutor. Such selective choices can be based on interaction or experience with individual conspecifics or individuals of other species that are accepted as tutors. Some species, for example bullfinches (*Phyrrhula phyrrhula*), nightingales (*Luscinia megarhynchos*) and European starlings (*Sturnus vulgaris*), learn songs even from a human tutor provided he/she has hand-reared them (review in Hultsch and Todt, 1998). The age of birds when interaction begins plays a prominent role in tutor acceptance (Baptista and Petrinovich, 1984).

In classical approaches, social factors were studied by testing individuals with only one particular experimental variable, e.g. a live tutor either present or absent (Baptista and Petrinovich, 1984, 1986, 1987; Marler, 1987; Marler and Peters, 1988). However, another experimental design deserves attention wherein birds are exposed to more than one learning experiment. Here individual birds experiencing different settings then express their preference for a setting by imitating songs heard in that particular situation (Hultsch and Todt, 1989; Todt and Hultsch, 1998). Application of this "choice design" has special advantages for species that, like nightingales, develop large repertoires of different songs (Fig. 1).

Here we review studies of nightingales exposed to such a "choice design" (Hultsch et al., 1999). Such studies, in particular, have addressed the role that social variables play when young individuals of both sexes were tutored with conspecific master songs. In addition, we report gender-related differences that become apparent among tutored subjects when they, as adults, are again exposed to the master songs. Our reports pay tribute to Luis Baptista and his valuable work on the learning and use of birdsong, on the diversity of song-related behaviors in males or females, and on their colorful distribution across oscine species (Baptista, 1996).
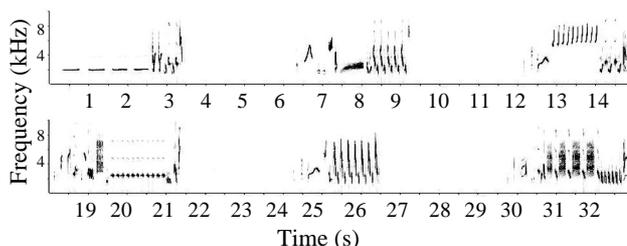

Fig.1　Frequency spectrograms of six songs in succession (section of a longer bout of singing) by a male nightingale
The vocal repertoire of an adult male comprises about 200 different types of songs, some of which may show similar patterns in the beginning (here: songs 3 and 5). Note: The first song is a "whistle-song" that serves to attract females (Hultsch 1980; see text).

2 Methods

2.1 Subjects

Our subjects were eight hand-reared nightingales. Shortly before fledging they were transferred to individual cages in a housing room where subsequent tutoring was conducted. At an age of three months, i.e., the time when occasional subsong begins, the birds were housed individually in sound proofed chambers.

2.2 Tutoring

Tutoring followed our standard experimental protocol. Subjects were exposed to different strings of master songs that served to label an experimental regime. Each string, or learning list, contained a different set of master songs drawn at random from our catalogue of song models that, in former experiments, had proven themselves as learning stimuli (Fig. 1). Selected songs were recorded on digital tapes with 4 seconds of silence between each (the typical duration of intersong intervals in nightingales). Each tape was presented twice at about one hour after light onset, on five successive days. Thus, the birds were exposed to every master song a total of 20 times. Two learning programs (PRESENT and INTERACT) were presented on the same day, with a silent interval of 10 minutes between them. Their presentations were reordered each day, and their procedures were as follows:

(1) PRESENT (control regime, familiar human tutor present). Five minutes before the start of training, the tutor entered the room to a position 2 meters from the birds and with a loudspeaker (Bose, Room Mate II) positioned in front of the him/her. From that position the tutor operated the playback of master songs (string: control). At the end of the playback the tutor remained seated for another 5 minutes. Behaviors of the tutor and bird were monitored and recorded audiovisually from outside the room.

(2) INTERACT (experimental regime, two human tutors present). The procedure here differed from (1) in the following details. Both a tutor familiar to the subject and one unfamiliar to it were present simultaneously during a training session, and positioned with their speakers in opposite corners of the room. During stimulus presentation, the birds were exposed to one long string of master songs. However, while this playback was running, either the right or the left speaker was activated, i.e., the birds heard selected songs (e.g., 1, 2, 3) only from the familiar tutor (on the right), and other songs (e.g., 4, 5, 6) only from the unfamiliar tutor (on the left side). To exclude serial effects, the successions of master song subsets were changed from day to day, i.e., the birds heard songs 4, 5, 6 ahead of songs 1, 2, 3.

2.3 Recording and analysis

Throughout song development (November to April) and later during adult male singing, vocal behaviors were automatically recorded by a computer-controlled registration using Panasonic Hi-fi F55 stereo video recorders and Sennheiser ME80 microphones. Recordings were analyzed by sound spectrography using the program "Avisoft" (R. Specht, Berlin). For the analyses we selected longer records of coherent singing (20 minutes or longer) and sampled at least a total of 2 hours of singing from each male. Due to the versatile singing style of nightingales, such sampling is sufficient to assess the complete repertoires of the birds. Spectrographic displays of song patterns were compared to spectrograms of the presented master songs by two independent persons who were not informed about the regimes in which master songs were played: see Hultsch and Todt (1989) for criteria used to identify a given song pattern as an imitation of a master song.

2.4 Testing of adult females

As they did not develop any song-like vocalization, females were tested further to determine how they were affected by the experimental variables. Females that had reached an age of about one year were exposed to a second playback of conspecific songs. Stimuli included (1) songs that had been tutored versus songs that were new for the birds, and (2) whistle-songs versus non-whistle-songs (Fig. 1, based on Metz (1998) for the whistle-songs). Experiments with other songs were conducted and evaluated accordingly.

The testing situation was a central home cage, which housed the subject and to which single cages were attached at either end. Thus, a test bird could move voluntarily between the middle cage and the two end cages which each held loudspeakers (Bose Roommate II) to present song playbacks simulating the singing of a male. To control for the influence of specific songs on the subject's responses, we prepared playback-tapes that each contained a different set of 10 song stimuli for presentation over a total of 10 minutes. All experiments were recorded by audiovisual equipment. Since females did not show copulation solicitation displays consistently, we analyzed spatial behaviors, i.e., movement rates, movement direction, and time-related features of spatial behavior. A movement was defined as a perch change or a jump on the ground (details in Metz, 1998).

2.5 Statistical analysis

Because movement patterns measured were not distributed normally ($P < 0.08$, with $P > 0.2$ safe), we used only ranked data. We did not run a Principal Component Analysis, because most measurements did not correlate with each other. Each movement pattern was tested separately. To detect any significant differences between responses to playbacks, a nonparametric ANOVA for related samples was used. The Wilcoxon-Single Comparison was applied to determine playback-trials that elicited responses detected by the ANOVA. P-values between 0.10 and 0.05 were regarded as trends, and P-values equal to 0.05 or lower were regarded as significant.

3 Results

3.1 Song learning

All males (*n*=4) developed songs that could be identified unambiguously as imitations of the master songs presented by a social tutor. Although there was inter-individual variation in the overall learning success, acquisition from the PRESENT-regime was in no case higher than from the INTERACT-regime, and two of the four males had acquired more imitations from the latter tutoring than the first (Wilcoxon matched pairs sign test, *n*=4, $P < 0.01$). A closer inspection of imitations derived from the INTERACT-regime showed that these birds had indeed preferentially copied master songs presented by the unfamiliar tutor. In contrast to males, none of the females developed any song-like vocalization, consistent with findings from other learning experiments with female nightingales.

3.2 Song performance

Analyses revealed two remarkable results. First, males sang imitations of songs presented by the unfamiliar tutor more frequently than those from the familiar tutor (Wilcoxon matched pairs sign test, *n*=4, $P < 0.05$). Secondly, song imitations were not given randomly but delivered instead in clusters derived separately from each tutor (Fig. 2), i.e., the birds performed imitations learned from one tutor in a single sequential block separated from sequences of imitations of the other tutor.

3.3 Female responses

Analysis yielded two results. First, we could not find evidence that the females discriminated between tutored and novel songs. Thus, it remained open whether the females remembered any cues from the tutoring programs experienced early in life. Secondly, however, females did discriminate clearly between two specific classes of nightingale song: whistle-songs and non-whistle-songs (Fig. 1).

In addition, females displayed a number of remarkable behaviors in preferential response to whistle-songs. When exposed to playbacks of conspecific song, adult fe-
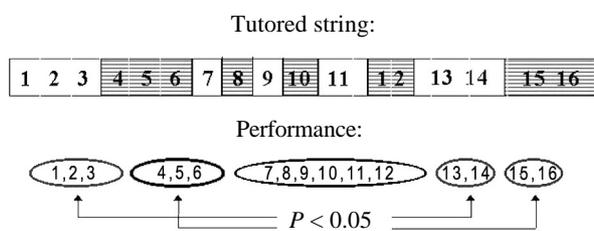
Tutored string:

Performance:

Fig. 2 Relationships between a string of master songs (top) and imitations developed by the birds (bottom)
Master songs were presented in an interactional learning regime: songs 1,2,3,7,9,11,13,14 were presented by the familiar tutor, and songs 4,5,6,8,10,12,15,16 by the unfamiliar tutor. During their performance, the imitations occurred sequentially clustered according to social origin; i.e. birds developed a sequential association among imitations 1,2,3,13,14 from one social source and another one among imitations 4,5,6,15,16 from the other source. This effect was not significant in imitations of songs that the birds had experienced from an immediate alternation of tutor roles (songs 7,8,9,10,11).

males neither vocalized nor gave soliciting displays, but instead performed particular movement patterns. There were more movements per minute during playbacks of whistle-songs than during other nightingale songs ($P = 0.026$). Females approached the compartment contiguous to the active speaker most quickly during playbacks of whistle-songs. Latencies tended to be shorter than latencies during playback of control songs ($P = 0.005$). The greatest number of movements towards the speakers happened during playbacks of whistle-songs. Difference from movements towards speakers during playbacks of control nightingale songs ($P = 0.015$) was significant. Females spent the longest time in the compartment connected with the active speaker during playback of whistle-songs ($P = 0.005$). Latencies to the perch next to the active speaker were also shortest during playbacks of whistle-songs ($P = 0.045$; further details in Metz and Todt, in prep.).

4 Discussion

4.1 Song learning

Social factors can influence the vocal learning of various bird species (Todt, 1975; Pepperberg, 1993; Baptista and Gaunt, 1997), including oscines (reviews in Kroodsma, 1982; Todt and Hultsch, 1998). In zebra finches (*Taeniopygia guttata*), for instance, social interaction with a live tutor is crucial (review in Tchernikowski et al., 2001). White-crowned sparrows (*Zonotrichia leucophrys*) are likewise sensitive to social stimuli (Baptista and Petrinovich, 1984), and they may even learn alien songs from live tutors while rejecting the same songs presented by tape playback alone (Baptista and Petrinovich, 1987). Moreover, species that develop large vocal repertoires, such as nightingales and European starlings, behave similarly; both accept a human caretaker as a social tutor (Todt et al., 1979; Boehner and Todt, 1996).

The results presented here supplement such findings by showing that nightingales can also learn from an unfamiliar tutor. This outcome suggests that "being reared by a human" may open a window of acceptance for "being tutored by another human". Enhanced song memorization and/or sensorimotor song learning in these trials may have been facilitated by variables that aroused the birds or their attention. This explanation agrees with results of other studies suggesting that an essential property of song factors may be their operation as attention or arousal mechanisms (review in Hultsch et al., 1999).

4.2 Song performance

Our study uncovered a relationship between specific properties of learning stimuli and the performance mode of learned songs. In the literature on song acquisition by oscines, this issue has been widely neglected. Nevertheless, it merits consideration because it points to both potential influences of intrinsic state variables, such as attention or arousal, and cognitive processes involved in song performance, such as a cue-related categorization of songs. Our birds uttered songs imitated from an unfamiliar tutor

more frequently than songs acquired from a familiar tutor, and at the same time sang imitated songs in clusters according to social origin. These results correspond to findings on the song performance of other nightingales that had been exposed to two different learning regimes, one in which the birds were tutored normally and the other in which they experienced auditory stimuli paired with specific visual stimuli, e.g., stroboscopic light (Hultsch et al., 1999).

Therefore, we conclude that stimuli which raise the attention or arousal levels of a given bird can facilitate the development and also the performance of specific vocal imitations. In functional terms, this implies that the mechanisms underlying such processing could indeed improve a given bird's outcome in song contests with rivals, as also would clustering song according to origin. The results suggest that the birds were indeed able to extract and memorize social information encoded in a given tutoring regime, and that they also used such information when organizing their song performance as adults. We assume that such a cue-related categorization of songs points to a cognitive processing of acquired song stimuli. This assumption is in line with predictions derived from an earlier study that provided evidence for the formation of so-called "context groups" (Todt and Hultsch, 1998). The results of that study indicated, as well, that such group formation reflected a process of categorization, such as sorting learned songs according to specific contextual cues. In the field, a repertoire performance following such cues could enhance a rapid addressee-related memory retrieval of specific types of songs. However these conjectures require further investigation.

4.3 Gender-related issues

Oscines vary remarkably in whether and how females develop a species typical song (Baptista and Gaunt, 1994). In some taxa, even closely related species may differ in a gender-related distribution of singing behavior. For instance, although sex differences seem clear in white-crowned sparrows where singing is specific to males, females of the sedentary race *Z. l. nuttalli* and the migratory race *Z. l. oriantha* can sing at certain times. In white-throated sparrows (*Zonotrichia albicollis*) that occur as white-striped and tan-striped morphs, moreover, females of white-striped morphs sing in the wild, but tan-striped females do not (reviews in Baptista et al., 1993; Baptista, 1996).

Given such gender-related differences of song learning and singing, we addressed this issue in nightingales and found that nightingale females neither learn nor vocalize conspecific songs. In addition, their behavior did even not reveal whether, as adults, they remembered songs heard during a tutoring experiment early in life, let alone discriminate such songs from completely novel ones. Although we cannot exclude the possibility that these results were affected by methodological factors, we nevertheless assume that they reflect some biologically meaningful differences. In a species like the nightingale, in which males sing large repertoires of songs and song learning is not constraint on a bird's natal summer, it seems prudent not to discriminate individuals by single types of songs. Rather, it would be wiser to identify a given male by his particular song sequencing, which provides a more reliable individual cue than a single song pattern (Todt and Hultsch, 1998).

Female nightingales were attracted to a special class of songs, namely whistle-songs, a resonse that may be species typical. Such a functional role of whistle-songs was postulated earlier by Hultsch (1980) who found this song to be given particularly frequently by unpaired males and predominantly when migrating females were returning to their breeding areas. This finding is a prime example of congruence in laboratory investigation and field study — something that the late Luis Baptista stressed as an essential aim in biological research (Baptista, 1996).

References

Baptista LF, 1996. Nature and its nurturing in avian vocal development. In: Kroodsma DE, Miller EH ed. Ecology and Evolution of Acoustic Communication in Birds. Ithaca: Cornell University Press, 39–60.

Baptista LF, Petrinovich L, 1984. Social interaction, sensitive phases and the song template hypothesis in the white-crowned sparrow. Anim. Behav. 32: 172–181.

Baptista LF, Petrinovich L, 1986. Song development in the white-crowned sparrow: social factors and sex differences. Anim. Behav. 34:1 359–1 371.

Baptista LF, Petrinovich L, 1987. Song development in the white-crowned sparrow: modification of learned song. Anim. Behav. 35: 964–974.

Baptista LF, Gaunt SLL, 1994. Advances in studies of avian sound communication. Condor 96: 817–830.

Baptista LF, Gaunt SLL, 1997. Social interaction and vocal development in birds. In: Snowden CT, Hausberger M ed. Social Influences on Song Development. Cambridge: Cambridge University Press, 23–40.

Baptista LF, Trail PW, Wolfe BB, Morton ML, 1993. Singing and its function in female white-crowned sparrows. Anim. Behav. 46: 511–524.

Boehner J, Todt D, 1996. Influence of auditory stimulation on the development of syntactical and temporal features in European starling song. Auk 113: 450–456.

Hultsch H, 1980. Beziehungen zwischen Struktur, zeitlicher Variabilität und sozialem Einsatz des Gesangs der Nachtigall (*Luscinia megarhynchos*). PhD thesis, Free University of Berlin.

Hultsch H, Todt D, 1989. Memorization and reproduction of songs in nightingales (*Luscinia megarhynchos*): evidence for package formation. J. Comp. Physiol. A 165: 197–203.

Hultsch H, Schleuss F, Todt D, 1999. Auditory-visual stimulus pairing enhances perceptual learning in a songbird. Anim. Behav. 58: 143–149.

Kroodsma DE, 1982. Learning and the ontogeny of sound signals in birds. In: Kroodsma DE, Miller EH ed. Acoustic Communication in Birds, Vol. 2. New York: Academic Press, 1–23.

Marler P, 1987. Sensitive periods and the role of specific and general sensory stimulation in birdsong learning. In: Rauschecker JP, Marler P ed. Imprinting and Cortical Plasticity. New York: John Wiley and Sons, 99–135.

Marler P, Peters S, 1988. Sensitive periods for song acquisition from tape recordings and live tutors in the swamp sparrow, *Melospiza georgiana*. Ethology 77: 76–84.

Metz M, 1998. Female choice in nightingales. Diploma Thesis, Free University of Berlin.

Pepperberg I M, 1993. A review of the effects of social interaction on vocal learning in African grey parrots (*Psittacus erithacus*). Netherl. J. Zool. 43: 104–124.

Tchernichovski O, Mitra PP, Lints T, Nottebohm F, 2001. Dynamics of the vocal imitation process: how a zebra finch learns its song. Science 291: 2 564–2 569.

Todt D, 1975. Social learning of vocal patterns and modes of their application in grey parrots (*Psittacus erithacus*). Z. Tierpsychol. 39: 178–188.

Todt D, Hultsch H, Heike D, 1979. Conditions affecting song acquisition in nightingales (*Luscinia megarhynchos*). Z. Tierpsychol. 51: 23–35.

Todt D, Hultsch H, 1998. How songbirds deal with large amounts of serial information. Biol. Cybernetics 79: 487–500.