Birds and babies : a comparison of the early development in vocal learners

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3 The interplay of perceptual predispositions and experience on song preferences and development in zebra finches (Taeniopygia guttata)

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Abstract

Vocal acquisition in songbirds and humans show many similarities, one of which is that both are driven by a combination of experience and perceptual predispositions (Bolhuis et al, 2010; Doupe & Kuhl, 1999). Among languages, some speech sounds are shared, while others are not. This could reflect a perceptual predisposition in young infants for learning some speech sounds over others, which combines with an exposure based preference to guide learning. Similarly, in songbirds some sounds are general across populations while others are more specific to populations or individuals. Here we examine whether this is also due to perceptual preferences for certain species specific element types in naïve juvenile birds and how such preferences interact with exposure to guide subsequent song learning. We show that young male zebra finches lacking previous song exposure perceptually prefer more common (general) over less common elements of species specific songs. This indicates a bias for within-species vocalizations, independent of exposure. Next we demonstrate that subsequent exposure to either common or to less common elements alters the birds' perceptual preference, resulting in a preference for tutor song elements. In adulthood, birds tutored with more common elements showed a higher song similarity to their tutor song, indicating that the early bias influenced song learning. Our findings help to understand the maintenance of vocal similarities, as well as the presence of differences, among birds' songs, their dialects and human languages.

Introduction

Vocal learning is essential for spoken language as well as for bird song, and the learning processes involved show many parallels (Bolhuis et al, 2010; Doupe & Kuhl, 1999). One interesting parallel is that both processes are guided by perceptual predispositions (i.e. perceptual biases independent of perceptual experience) that interact with experience. While presence of this interaction is broadly accepted, debate and discussions concern the nature of the predispositions and of the interaction in shaping vocal production (Adret 2004; Woolley 2012). In this paper we address these questions for a songbird species, the zebra finch.

The presence of predispositions in vocal learning is suggested by the distribution of sound patterns within and between populations. In human languages, some sounds are more or less universally shared, suggesting a possible predisposition for such sounds, while others are more language specific. Similarly, different populations of the same songbird species can share elements, but also sing different 'dialects' and song elements (Kroodsma et al, 1999; Marler & Tamura, 1964; Petrinovich & Baptista, 1984). In addition to geographic variation, song can also differ between individuals. Zebra finch song, for instance, consists of different types of elements (fig 3.1) and birds may vary in which elements are used and how they are combined. Some element types are more common across individuals than others. A recent study of song elements present in 13 different zebra finch populations showed that, although all element types occur in all populations, the proportion of some elements varied between populations whereas other elements are more equally present across populations. Also, individuals within a population can differ substantially in which elements they share or not (this thesis, Chapter 4). These differences on population and individual level have implications for understanding both development and evolution of learned vocalizations. Patterns or elements that are common across individuals and populations might indicate species general predispositions facilitating selective learning and constraining vocal variation. The population or individually specific elements might not be based upon such predispositions but arise from plasticity in the learning process, allowing deviating elements to develop and be learned and maintained by cultural transmission. In such a scenario, predispositions for common elements would likely be present early in development before song exposure, guiding the learner to particular conspecific sounds. Preferences for less common elements are expected to emerge later on as a result of experience.

Evidence for predispositions so far has mainly come from experiments showing a preference to learn conspecific sounds over heterospecific ones in studies involving isolate rearing and tape tutoring. In most studies adult song production is used as a measure of learning or selective preference. Only few studies have examined perceptual predispositions in naïve birds. An experiment in which juvenile zebra fiches (*Taeniopygia guttata*) could elicit exposure to either conspecific or heterospecific song by hopping on a perch showed that birds hopped more on the perch generating conspecific song than on the one for heterospecific song (Braaten & Reynolds, 1999). In another species, the white-crowned sparrow (*Zonotrichia leucophrys*), fledglings produced more begging calls in response to conspecific song than to heterospecific song (Nelson & Marler, 1993; Soha & Marler, 2001). Preference for the own subspecies over other subspecies was not confirmed, but exposure to songs of the own subspecies lead to better discrimination than experience with another subspecies' song. This outcome suggests that the perceptual system is more attuned to acoustic features of the own subspecies (Nelson, 2000). Moreover, the universal white-crowned sparrow's introductory whistle has been shown to function as a cue for song learning, since songs (even heterospecific ones) are better copied when they contain these universal whistles (Soha & Marler, 2000). This suggests that in addition to a preference for conspecific versus heterospecific vocalizations, there are predispositions for certain *within-species* element types. This has also been shown in a study on grasshopper sparrows, showing that naïve female fledglings respond more to one conspecific song type ('buzz' simple structure and uniform across individuals) than another conspecific one ('warble', complex and possibly individually specific) (Soha et al, 2009).

While the above mentioned studies suggests the presence of *within species* perceptual predispositions in male songbirds, clear demonstrations of their presence are lacking, as well as insight in the effect of later exposure on perceptual preferences. Moreover, little is known about the relative effects of predispositions and exposure on later song production. In the present study we address these questions. Perceptual preferences are tested in juvenile male zebra finches at different stages of development. By testing the birds before hearing song and by manipulating subsequent exposure, we disentangle the effects of possible predispositions and auditory song experience. We also examine the similarity of the acquired songs to those heard during exposure and discuss how predispositions and vocal learning relate to the distribution of song elements over populations and individuals.

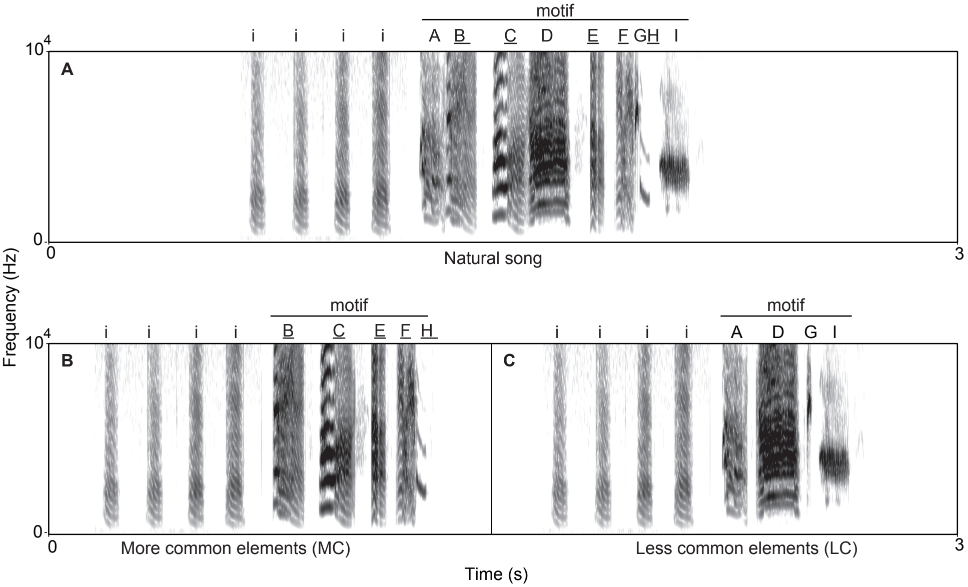

Figure 3.1. Examples of one pair of stimuli, constructed from one original song (**A**). From the original song, more common (MC) element types were selected (indicated by underlined letters) and combined into an artificial 'common song' stimulus (**B**) and similarly 'uncommon' song stimuli were constructed (**C**) using less common (LC) elements of the same original song. Both stimulus types started with four introductory notes from the original song (indicated by 'i').

Results

Perceptual preference for more common element types in male birds naive to song

Juvenile male zebra finches were reared by their mother only, from approximately 8 dph (days post hatch), well before the start of the sensitive phase for song learning (Eales, 1985; Eales, 1987; Jones et al, 1996a). As female zebra finches do not sing, we thus created relatively natural rearing conditions where zebra finches are not exposed to song. The birds were tested at 37 dph (+-2d) when they were naive to song, to see if they have a preference for more common or less common elements (see methods for details).

The classification of elements as common or not, was based on literature describing the element types found across several populations (Holveck et al, 2008; Leadbeater et al, 2005; Sturdy et al, 1999; Zann 1993) or reporting rare elements ((Leadbeater et al, 2005), see methods and SI table 1). Based on this classification, we created two paired stimuli from each one of eight original natural songs. The more common elements of a song were selected for constructing a 'common song'. The less common elements of the same original song were used to construct the 'uncommon song' (fig 3.1). Each bird was tested with four pairs of common and uncommon songs on the same day.

The results show that juvenile males significantly prefer common songs over uncommon ones (n=12, deletion $p < 0.01$, SI, fig 3.2). So, initially, before song exposure, males have a bias for more common zebra finch song element types.

Preference for tutor song at 57 dph

After the 37 dph preference tests the birds were exposed to (tutored with) either a common or an uncommon song until approximately 67 dph. The tutor songs were selected from the same set of stimuli used for the preference test and each bird was tutored with a different song. The preference tests were repeated at 47 (+-2) dph and 57 (+-2) dph in order to test the effect of the subsequent exposure on the birds' preferences. Each preference test again consisted of four blocks (four pairs of common versus uncommon song), one of which included the tutor song. By comparing preference for the pair including

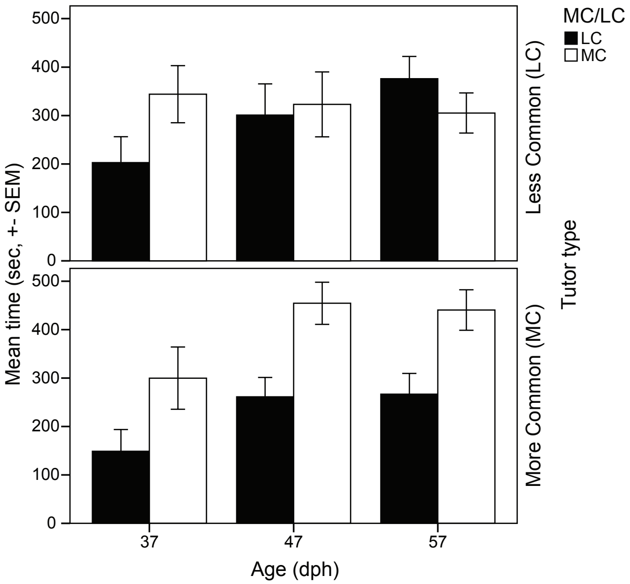

Figure 3.2. Preferences independent and dependent of song exposure. The preference measured is time in seconds (+-SEM) near the speaker broadcasting songs constructed with more common elements (MC) or songs constructed with less common elements (LC) for zebra finches at 37 dph (before tutoring, see methods). This preference is higher for more common elements (white bar) then for less common elements (black bar). At 57 dph (after tutoring) birds prefer the type of sounds they have been tutored with; birds tutored with more common elements (lower panel, MC) prefer songs with more common elements and birds tutored with less common elements (top panel, LC) preferred less common element types.

the tutor song to the other three pairs, we could test whether the preference at 57 dph was specific for the tutor song only or that other songs of the same type (common/uncommon) are preferred.

A significant 4-way interaction was found between preference (common/uncommon song), age (37,47, 57 dph), tutor type (common/uncommon song) and block (tutor/non-tutor). This indicates that the preference changes with age, depending on the type of tutoring and whether it is the tutor song or not (n=16, deletion $p < 0.05$, fig 3.2, SI). Since 4-way interactions can be hard to interpret and to confirm the interactions at lower levels, separate analyses at 57dph, when the interactions at expected. This revealed a significant interaction between preference and tutor type at 57 dph for the blocks including tutor songs (n=13, deletion $p < 0.01$), but not for the other three blocks (n=16, deletion $p > 0.05$), suggesting that the later preference was specific to the tutorsong. When we look at the two tutor groups separately the interaction between preference and block (tutor/non-tutor) was significant for both the birds tutored with common songs (n=8, deletion $p< 0.01$) and birds tutored with uncommon songs (n=8, deletion $p < 0.05$, fig. 3.3). These findings indicate that birds specifically prefer their tutor song (and thus song exposure) at 57 dph, in line with previous findings in adult birds (Houx & ten Cate, 1999a,b, Riebel et al, 2002).

Experience affects song learning.

After the last preference test at 57 dph the birds were tutored in isolation for 10 more days. Adult birds' songs were recorded (approximately 120 dph or older (Jones et al, 1996b)) and similarity between the pupils song and the tutor song was measured using Sound Analysis Pro software (SAP (Tchernichovski et al, 2000)).These measurements revealed that the pupils' song similarity with the tutor song was higher than similarity with a control song of the same type (common/uncommon song, paired Wilcoxon: n=16, $p < 0.05$), confirming earlier findings that experience leads to song copying. We also compared similarity with the tutor song to similarity with its counterpart, derived from the same original natural song but belonging to the other song category (fig 3.1). Thus for song from a pupil tutored with common songs (fig 3.1b), a comparison was made for similarity with the common tutor song (fig 3.1b) and the uncommon counterpart of that song (fig 3.1c, and vice versa for the pupil tutored with uncommon song). This comparison revealed an overall tendency for higher similarity with the tutor song than with its counterpart (paired Wilcoxon: n=16, $p = 0.06$). Most noticeable, however, was the tutor group difference found for this latter comparison. Pupils tutored with common songs showed higher similarity with the tutors than with their counterparts (paired Wilcoxon: n=8, $p = 0.02$), whereas this difference was not significant for the group tutored with uncommon songs (n=8, $p > 0.05$, group difference: Kruskal-Wallis: n=16, $p= 0.02$). In other words, evidence for similarity with the tutor song is stronger for pupils tutored with common song.

Discussion

Our findings suggest that juvenile birds naive to song have perceptual predispositions, making some elements more attractive than others. In addition to this, we show that these perceptual preferences can be modified by exposure, even resulting in a preference for initially non-preferred elements. Furthermore, while young birds can incorporate both types of song elements in their later songs, common elements are more likely to be copied.

Altogether, these observations provide evidence of a mechanism that may explain the species wide presence and maintenance of particular types of elements in a vocal learning species as follows. The perceptual bias present in naïve juvenile males can guide the learning process, directing the learners' attention towards particular conspecific vocal elements. This is likely to result in including these element types in the birds' later song production. The result of this process will be that these elements are more likely to be maintained in a population and hence become, or stay, more common. Over generations this process is likely to cause stabilization of vocal patterns containing these common features. There is an interesting parallel here with a mechanism that has been proposed for language which has described in terms of markedness, suggesting unmarked

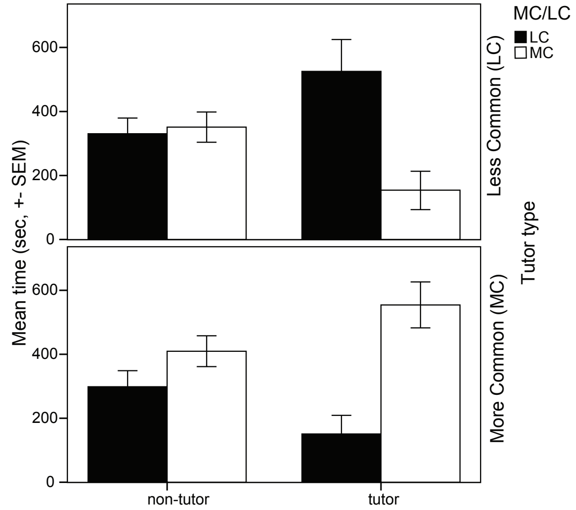

Figure 3.3. Specific preference for tutor song at 57 dph. Birds tutored with songs containing less common elements (top panel, LC) as well as birds tutored with songs containing more common elements (lower panel MC) prefer their tutor song. Birds lost their initial preference, thus they do not show a preference for common or uncommon songs that were not their tutor song.

('universal') sounds are acquired early in development and marked ones later. Unmarked sounds are more likely to (re)occur and to be maintained in languages. Acquisition of unmarked sounds (De Lacy, 2006), similar to acquisition of common song elements, might be driven by processes independent of linguistic input (Jakobson, 1941).

In addition to processes resulting in song conformity, if a young bird is exposed to elements for which there is initially no perceptual bias, this exposure can still result in copying such elements. This may result in song variation, and the appearance and maintenance of these elements in a population might depend on local factors and chance (drift) affecting cultural transmission.

Interestingly, our study provides empirical support for a mechanism suggested by a study by Feher et al., that elegantly showed a process of vocal convergence on more common, species specific, song features over generations (Feher et al, 2009). Zebra finch males reared without song exposure which produce aberrant song were used as tutors for a second 'tutor generation'. These latter birds were again used as tutors for a third tutor generation and so on. By three to four generations, songs had evolved towards songs with wild type characteristics. The tutees copied most of the elements of the aberrant song, but also induced alterations to their tutor song. Due to accumulation of these alterations over tutor generations, the songs in the later generations became more similar to wild type songs. We suggest that the biases we demonstrated affected the direction of element deviations, driving them towards becoming more similar to preferred (and also more normal and common) elements. While the observed bias is independent of song exposure, we cannot fully exclude that it is fully independent of any acoustic exposure, as it may have been affected by the mothers' vocalizations during rearing. Even though females do not sing they do produce calls that may affect the auditory preferences. There is some evidence for perceptual preferences being formed before 35 dph (Clayton, 1988; Roper & Zann, 2006). The female's call has some features in common with some of the more common elements (stacks) but certainly not all of them (for instance slides). Future research could elucidate this issue by examining in more detail which specific acoustic features make certain element types attractive and by using muted females to rear the subjects. Regardless of the cause of the sensitivity, the effect of the bias is independent of *song* exposure and thus remains relevant in terms of development and evolution and may result in maintenance of such sounds in a species.

While the present experiment can provide insight in the evolutionary consequences of the perceptual biases and the developmental processes involved, less can be said about the evolutionary origin of the perceptual biases. Nevertheless, our findings may be interesting for future research on mate attraction. In zebra finches songs are supposed to function primarily in mate choice and pair bonding. There is ample evidence that female zebra finches prefer specific songs or song features over others (Riebel, 2009). These preferences may concern the presence of certain general features of songs. For example, naïve and normally reared female zebra finches prefer conspecific song (Braaten & Reynolds, 1999; Lauay et al, 2004), which might help to maintain the species specificity of male songs. On the other hand, females prefer tutored song (normal quality) song over untutored song (abnormal quality, (Lauay et al, 2004)) and larger repertoires over smaller ones (Holveck & Riebel, 2007). This might drive the use of additional uncommon song elements and thus male song plasticity, since tutored song requires experiences and larger repertoires are more likely to include more uncommon elements in addition to the common ones. However, little is known about specific element types being preferred by females and how the presence of these contributes to attractiveness of the song as a whole. It is known that females don't systematically prefer songs with expiratory elements (classified as common) over songs with inspiratory high notes (here classified as uncommon, (Leadbeater et al, 2005)), but it would require more specific tests to examine whether female zebra finches differentially prefer (songs with) common or uncommon elements, to get insight in the evolutionary dynamics from which the current male songs have arisen.

The finding that both an initial bias for more common elements and later experience affect song learning has a striking parallel in human infants. In infants, early phonemic discrimination is universal and becomes more language specific later on (Tsao et al, 2006). A similar developmental change can be observed for acquisition of syllable structure. In early language productions the first syllables are of the CV (consonant-vowel) type which is common across different languages. Subsequent development of novel syllable types is influenced by frequency of occurrence and may therefore also be experience dependent (Levelt et al, 2000). Although there is a clear parallel, the distinction between more and less common elements is somewhat different from that between universal versus non-universal speech sounds in humans. In zebra finches there are clear individual differences within populations, while differences in sound inventories between populations are less clear (this thesis, chapter 4). In contrast, human speech sound inventories differ between languages and people speaking the same dialect usually make use of approximately the same phoneme inventory. It should be noted however, that the use of different analytical methods for human language and birdsong makes a direct comparison difficult. Thus the developmental mechanism may be similar (attention changing from more common to less common, i.e. from internal biases to external influences), but the eventual effect of the developmental plasticity due to the vocal learning may differ between humans and songbirds. If the developmental mechanism is indeed the same for birds and humans, the implications described above may also hold for language evolution. Initial biases could maintain the universals in languages whereas additional plasticity allows for learning language-specific patterns and facilitates cultural evolution.

Material and methods

Subjects and housing
For the experiments 16 male wild-morph domesticated zebra finches from an out bred breeding colony at Leiden University, the Netherlands, were used. The birds were kept at 20-22 °C and 55-65 % humidity on a light dark schedule of 13.5:10.5 hours. Food, water and a cuttlebone were available ad libitum.

At the age of 8 dph (± 2) the young birds and their mother were moved into a room where no adult males were present. At the age of 37 dph (± 2) the birds received the first preference test. Each bird was moved to the preference cage the day before the test in order to acclimatize to the new cage and to isolation. After the test, the birds were isolated in sound attenuated chambers for song exposure. In the sound attenuated chambers food, water and cuttlebone was available ad libitum. The light dark schedule in the sound attenuation chambers was 13.5:10.5 hours with a temperature of 21-24 °C and a humidity of 50-55 %. The experiment was approved by the Leiden University Committee for Animal Experimentation (DEC) under proposal number 10043.

Stimuli
The classification of elements as common or not, was based on literature describing the element types found across several populations (Holveck et al, 2008; Leadbeater et al, 2005; Sturdy et al, 1999; Zann 1993) or reporting rare elements (Leadbeater et al, 2005). These data are summarized in SI table 1 which was used to estimate which elements were more or less common among populations or individuals. As can be seen in SI table 3.1, the frequencies are rather a continuum than discrete distinction between common and uncommon. However we can estimate that stacks, slides, short slides and tones are in general more common elements and high notes (especially inspiratory ones), trills, high sweeps and noisy elements and elements that do not clearly fall into a category, are less common.

Elements were used to construct ‘common’ and ‘uncommon’ songs from natural songs produced by normally reared birds in the Leiden University zebra finch colony. From each of 8 natural songs, two versions of a motif were created: one ‘common’ version, using the common elements of the song and one ‘uncommon’ version using the uncommon elements from the same original song (fig 3.1). This way, individual factors like voice characteristics cannot be the cause of the difference in preference between common and uncommon stimuli. Each stimulus song consisted of 4 introductory notes followed by 5 motifs.

The stimuli used for the preference tests and for exposure were modified by using Praat sound analysis software (version 5.1.41 for windows) and had a mean motif duration of 0.385s (range 0.284-0.519 s) for common songs and 0.379 s (range 0.276-

0.548 s) for uncommon songs. All 16 stimuli were rms equalized.

Exposure

The birds remained in isolation in sound attenuated rooms while tutored with either ‘common’ or ‘uncommon’ song via a speaker. The amount of exposure for all birds was the same (approximately 180 bouts per day, of five motifs per bout).

After the first day of preference testing, the birds were moved to a sound attenuated isolation chamber where exposure (tutoring) started the next day. Every bird was tutored for approximately 20 times per hour (random timing) during 7.15 h and 13.15 h and 10 times per hour during 13.15 h and 19.15 h. Thus the amount of exposure for all birds was the same ((6hx20=) 120 + (6hx10=) 60)=180 bouts per day, of five motifs per bout). Birds were tutored each day from age 37 dph to 67 dph, with exception of the days of preference testing.

Preference tests

Birds were tested for their preference at 37 dph (before tutoring started), 47 dph and 57 dph, each time using the same four sets of stimuli (i.e. the same blocks, see below), including the stimuli to which the birds were exposed during the tutor phase.

Preferences were measured using a phonotaxis setup (Holveck & Riebel, 2007); a cage with one speaker on each side, alternating song playbacks with more common element types from one speaker and less common element types from the other. The time spent on the left and the right side of the cage was used as a measure of preference (measured from the first response after playback). When the birds were in the centre of the cage (a neutral zone) this was not included in the response time. Each test consisted of 4 blocks on one day (always in the morning when birds were most active), each block with a different pair of common and uncommon stimuli. Thus two sets of 8 stimuli (4 pairs of common and uncommon song) were used, 8 birds were tested with the first set and 8 birds with the second set.

One block consisted of 14 minutes alternating each minute between common song from one speaker and uncommon song from the other speaker. Each minute contained 7 identical songs. The order of the type of stimulus and side from which they were played back was counterbalanced between blocks and between subjects. Songs were broadcast at approximately 70db. After each block, the bird had a break of 45 minutes before the next block started.

Video recordings of each test were analyzed while blind to the stimuli using ELAN software (version 3.8.1 http://www.lat-mpi.eu/tools/elan/, Max Planck Institute for Psycholinguistics, The Language Archive, Nijmegen, The Netherlands, (Sloetjes & Wittenburg, 2008)). When birds did not show any response during a given block, this block was excluded from further analysis. Due to the lack in response in all 4 blocks, 4 birds had to be excluded from the 37 dph analysis, thus this analyses was based on 12 birds.

Song analysis

Birds' songs were recorded at age 120 dph or older (when they did not sing at 120 dph). From each bird the predominant motif was selected and similarity measures between the subject's song (pupil) and the artificial tutor song were measured using Sound Analysis Pro (SAP2011, (Tchernichovski et al, 2000)).

Statistics

All statistical analyses were performed using R version 2.11.0. Linear mixed effect models were performed for preference test data using the nlme package for R, version: 3.1-96 (Pinheiro et al, 2009). Subject was included as a random factor, with 'block' (the four songs tested per bird per age) nested within bird. Deletion p-values were accomplished by comparing models with and without the variables of interest using the anova method in R. Model assumptions (normally distributed errors and lack of heteroscedasticity) were always verified after model selection.

Statistical analyses for song similarity measures were performed using Wilcoxon Signed Rank tests and Kruskal-Wallis rank sum tests.

Acknowledgements

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SUPPLEMENTARY INFORMATION

Sturdy et al. 1999	JH	QB	R	QP	**Leadbeater et al. 2005**		**Zann 1993**		**Holveck et al. 2008**		**Price 1979**	
	*	*	*	*		#		*		*		*
combination note	36	3	4	14	combination note	60	distance call	16	-		long call	27
slide note	9	35	22	16	slide note	95	downslur	2	down sweep	53	-	
flat note	9	20	21	10	flat note	90	tone	1	tone	17	medium call	9
							stack	17	stack	9		
short slide	37	35	44	44	-		introductory element	24	-		short call	31
							introductory diad	2				
high	9	7	9	16	inspiratory high	45	high	10	high	3	non-call type	32
					expiratory high	60			high sweep	1		
-					noise	10	noise-noise	7	noisy	11		
							noise-structure	*4*	short noisy	1		
							ladder-noise	*4*				
							tone-niose	*3*				
							noise-DC	*3*				
							noise-tone	*3*				
							n-n-DC	*1*				
-					buzz	5	-		trill	3		

SI Table 1. **Elements described in the literature**. The different studies used different classification systems causing some categories to fall into two categories in one study and into one category in another study (for instance inspiratory and expiratory high notes in Leadbeater et al., are grouped in to 'high notes' according to Sturdy et al.'s classification). In order to compare studies, Sturdy et al. is used as a reference point and element types on the same row are expected to be similar to a certain extend. This table was used as an estimate to classify elements into 'more' or 'less' common for constructing the stimuli. Frequency of note types from different colonies are given in %, (* : % of total number of elements, #: % of motives containing a specific element). The investigated colonies are from Pennsylvania, U.S.A. (Price, 1979), Alice Springs and Murray River, Australia (Zann, 1993; Zann, 1996), Utah, U.S.A. (Leadbeater et al, 2005), Leiden, the Netherlands (Holveck et al, 2008) and the following 4 colonies by Sturdy et al. (Sturdy et al, 1999): JH: John Hopkins, QB: Queen's biology, R: Rockefeller, QP: Queen's psychology.

Statistical details

Preference test 35dph

16 birds were tested, of which 4 did not show a response and had to be excluded. When a bird sat on the same perch during a whole test this was counted as a lack of response and the test was excluded. Several blocks (one of the 4 tests on one day) also had to be excluded due to lack of response. Statistics were performed on the remaining 12 birds with 27 blocks in total (blocks

were excluded when birds showed no response at all).

A linear mixed effect model was performed with time spent on each side of the cage as dependent variable, stimulus type (common/uncommon) as fixed factor, subject as random factor and block nested within subject.

Results for model comparison with (model2) or without (model1) stimulus type are listed below:

	Model	df	AIC	BIC	logLik	Test	L.Ratio	p-value
model1	1	4	740.2076	748.1635	-366.1038			
model2	2	5	735.3988	745.3437	-362.6994	1 vs 2	6.808736	0.0091

Preference test from age 35dph to 55dph

A linear mixed effect model was performed with time spent on each side of the cage as dependent variable, stimulus type (preference test common/uncommon), tutor type (common/uncommon), age (35,45,55dph) and tutor/nontutor as fixed factors, subject as random factor and block nested within subject.

Model comparison for an interaction between stimulus type x tutor type x age x tutor/non-tutor:

	Model	**df**	**AIC**	**BIC**	**logLik**	**Test**	**L.Ratio**	**p-value**
model1	1	25	3444.145	3532.181	-1697.072			
model2	2	27	3441.838	3536.918	-1693.919	1 vs 2	6.306308	0.0427

Age 55

Since a 4-way interaction was found, data were split in order to inspect the 55dph in more detail. A linear mixed effect model was performed with time spent on each side of the cage as dependent variable, stimulus type (common/uncommon) and tutor/nontutor as fixed factors, subject as random factor and block nested within subject.

Model comparison for an interaction between stimulus type x tutor type x tutor/non-tutor:

	Model	**df**	**AIC**	**BIC**	**logLik**	**Test**	**L.Ratio**	**p-value**
model1	1	4	1606.046	1617.06	-799.023			
model2	2	11	1598.321	1628.611	-788.1607	1 vs 2	21.7246	0.0028

We further spilt up the data to see if the difference between tutor song and non-tutor song stimuli was similar for birds tutored with common song and those tutored with uncommon song.

Model comparison for the group tutored with common songs testing for an interaction between stimulus type x tutor/non-tutor:

	Model	**Df**	**AIC**	**BIC**	**logLik**	**Test**	**L.Ratio**	**p-value**
model1	1	4	778.9096	787.011	-385.4548			
model2	2	7	772.4299	786.6074	-379.2149	1 vs 2	12.47972	0.0059

Model comparison for the group tutored with uncommon songs testing for an interaction between stimulus type x tutor/non-tutor:

	Model	**df**	**AIC**	**BIC**	**logLik**	**Test**	**L.Ratio**	**p-value**
model1	1	4	835.0433	843.4207	-413.5216			
model2	2	7	831.7837	846.4441	-408.8919	1 vs 2	9.259555	0.026