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Horizontal transmission of the father's song in the Zebra Finch (*Taeniopygia guttata*)

Sébastien Derégnaucourt[1,2,*] & Manfred Gahr[1]

[1]Department of Behavioural Neurobiology, Max Planck Institute for Ornithology, Seewiesen, Germany

[2]Laboratory of Compared Ethology and Cognition, University Paris West, Nanterre, France

* Corresponding author: Laboratoire d'Éthologie et Cognition Comparées, Université Paris Ouest, 200 avenue de la République, F92001 Nanterre Cedex, France.

Phone: +33-1-40-97-74-77. Fax: +33-1-40-97-74-74.

Email: sebastien.deregnaucourt@u-paris10.fr

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Abstract

As is the case for human speech, birdsong is transmitted across generations by imitative learning. Although transfer of song patterns from adults to juveniles typically occurs via vertical or oblique transmission, there is also evidence of horizontal transmission between juveniles of the same generation. Here, we show that a young male zebra finch (*Taeniopygia guttata*) that has been exposed to its father during the sensitive period for song learning can lead a brother, that has never heard the paternal song, to imitate some sounds of the father. Moreover, song similarity between the two brothers was higher than the similarity measured between the paternal song and the song of the brother that had a weeklong exposure to the father. We speculate that the phenomenon of within-generation song learning among juveniles may be more widespread than previously thought and that when a juvenile evaluates potential models for imitative learning, a sibling may be as salient as an adult.

1. Introduction

Socially meaningful interactions between juvenile animals are an everyday occurrence. In humans, research has shown that infants treat peers as social partners [1]. Juvenile stages are characterized by intense learning, and language acquisition has received particular emphasis [2]. Although language is unique to humans, one of its main components – vocal production learning – is shared with a few animal species. Prominent among these, oscine songbirds learn their species-specific song patterns by memorizing and imitating the songs of adult conspecifics. Some songbird species learn their song during a sensitive period early in life (age-limited learners) while others can learn throughout life (open-ended learners, [3]). The sensitive period of song learning is composed of two phases: a sensory phase and a sensorimotor phase. During the sensory phase, the bird memorizes the acoustic characteristics of the song model; during the sensorimotor phase, the bird uses this auditory memory as a template with which to compare auditory feedback from its own song during the imitative learning process [2,3]. Although young birds learn most of their vocalisations from adults, there is evidence - both from the field and the laboratory - that they can learn from conspecific peers as well [4-6]. In most species studied so far, depriving juveniles of adult song leads to abnormal song development [3]. If a young male zebra finch (*Taeniopygia guttata*) is raised alone with its father, it will develop a song that is a close copy of the paternal song [7,8]. However, in the absence of an adult model, untutored juvenile male zebra finches raised in a group will learn song from each other. Indeed, even in the presence of an adult male, juveniles can influence each other's song development. The more male siblings there are in a clutch, the shorter the mean duration of their song motifs and the fewer of their fathers’ syllables they imitate, revealing a fraternal inhibition of imitation of the father’s song [7]. When young zebra finches can interact freely with peers and adults, juveniles that associate most closely present common song elements [9]. Similarly, in starlings (*Sturnus vulgaris*) juveniles are much less likely to copy adult songs in the presence of peers [10]. These studies suggest that peer experience can affect song learning from adult models. In the present study, we further explore the relative influence of adult and juvenile models by asking whether a young bird, exposed to the song of its father during the early phase of the sensitive period, could lead one of its brothers to imitate the paternal song.

2. Material and methods

We used male zebra finches from the breeding colony of Seewiesen, Germany and the experiment described was approved by the government of Upper Bavaria. Breeding pairs were raised in separate cages in a common room. Chicks were raised by both parents until 14 dph (day post hatch) when the mother and her offspring were moved together into an isolation room in order to prevent young males from imprinting on their father's song. It has been shown that no memorization of a song model can occur in this species before at least 17 dph and that little, if any, occurs before song production starts around 25 dph [11].

At 35 dph, for clutches containing at least 2 males, one male was placed in a sound-attenuating box ("son # 2") whereas one of its brothers ("son # 1") was put back with his father for a week (n= 9 pairs). We chose this time period for two reasons. First, it is likely that this duration is long enough for the young bird to memorize its father's song. Second, based on previous recordings [12] we estimated that this time frame would not be long enough for the young bird to start producing a canonical version of its song motif resembling an adult model. A week later, the young male that was kept with its father was moved into the same cage as its brother in the sound-attenuating box. Both birds stayed together until 100 dph when they were separated to record their individual song, which is known at this stage to stabilize and which will exhibit no significant changes during the remainder of the bird's life.

Adult male zebra finches produce a 0.5-1.5-s song motif that is repeated several times during a bout of singing (Fig. 1; [13]). The motif is composed of a few syllables repeated in a fixed order. Syllables are highly stereotyped and often contain a combination of different sounds, usually called notes, with fast transitions (on a 10-ms timescale). Song of each individual bird was recorded using the Sound Analysis Pro software (SAP 2.062; freely available at http://soundanalysispro.com/). The program was run on a PC equipped with an Edirol UA1000 sound card (16 bits, 44.1 kHz), connected to multidirectional Earthworks TC20 microphones (one per sound-attenuating box) placed above the cage. Files containing song phrases were detected using Sound Explorer (developed by R. Jansen, Univ. Amsterdam) and song motifs selected for each bird. We measured similarity between song motifs using an automated procedure implemented in SAP that parametrically quantifies the similarity between songs [14]. This quantification is based on five acoustic parameters: pitch, frequency modulation, amplitude modulation, goodness of pitch and Wiener entropy. Based on these features, the procedure detects similar sections between songs automatically. Using the batch module of SAP, we computed 100 comparisons for each triad (father and sons). More details about the sound analysis are provided as electronic supplementary information. Raw data are available at doi:10.5061/dryad.7137r

3. Results

In many cases, we found clear evidence of a father's song syllables in the song of the son that was never exposed to him during the sensitive period ("son # 2"; Fig. 1). Therefore, this son learned these sounds by imitating the brother ("son # 1") that was raised with the father from 35-42 dph. The son that was exposed to the father produced a better copy of the paternal song than its brother (Fig. 2, Wilcoxon, p= 0.027). Nevertheless, its song was more similar to the song of its brother than to the song of their father (p= 0.02). Similarly, the song of the unexposed brother was more similar to the song of its brother than to the song of their father (p= 0.004).

We also observed that the more the exposed juveniles learned from their father, the higher the similarity was between their brother's (who never had contact with the father during the sensitive period) and their father's songs, although this trend was not significant (Spearman, Rho= 0.57, p= 0.12).

4. Discussion

This study shows that a young songbird exposed to its father during the early phase of the sensitive period can lead one of its siblings raised in isolation to imitate the paternal song. We observed a huge inter-individual variability in the number of sounds copied from the father's song, even among sons that were directly exposed to the father during the sensitive period ("son #1"). Moreover, in many cases, songs produced by the two brothers exhibited more similarity to each other than to father's song.

This last result confirms that zebra finch siblings can influence each other's song development even after exposure to an adult song model [7,9]. Sounds produced by siblings that cannot be found in their father's song might have been invented or improvised but could also result from errors in copying some sounds produced by their father [8]. Based on another laboratory experiment showing that song convergence can occur in young male finches raised in the absence of an adult model [4], it is likely that this result can even be extended between unrelated same-age peers that are.

Sounds from the paternal song could be found in the song motif of the son that was not exposed to its father during the sensitive period. This result demonstrates that learning of these paternal sounds was acquired through exposure to approximate second-hand representations of the model presented by the son that was exposed to the father during the sensitive period. To our knowledge, there is little evidence to indicate that exposure to same-age peers facilitates language acquisition through a similar process in human infants, although infants have a visual preference for peers of the same age, which may facilitate imitation [15]. However, it is known that children can have an impact on each other's language acquisition, such as in the case of the emergence of creole languages (whether spoken or signed) among children exposed to pidgin [16].

We observed a huge inter-individual variability in the success of the imitation of the adult model, namely the father's song. We chose to use sibling pairs and to raise one of them with the father, expecting that vocal sharing would be facilitated between kin for social reasons and not necessarily for genetic reasons since it has been shown that classical song features such as song length or repertoire size exhibit very low heritabilities [17]. Although vocal sharing was high between the two brothers, learning from the father was never perfect, often incomplete and in a few cases almost absent. There are several potential explanations for this result. First, the father did not feed its chicks after 14 dph. Since Immelmann's pioneering studies in this area [18], it has been assumed that one of the most important factors in the selection of a zebra finch song model is the close interaction between a young male and the male that rears it, generally its father. Second, one week of exposure might be insufficient to induce the close-to-perfect vocal imitation that is observed in most cases in which a young bird is raised with an adult until adulthood [8]. Nevertheless, it is known that short exposure to song models is sufficient to induce significant learning in oscine songbirds [3] including zebra finches [19]. Third, the relationship developed between the two siblings might have overridden learning from the father for the son that was exposed to him from 35-42 dph.

Even if the present work is completely artificial, it can have implications for the dynamics of natural populations of zebra finches. Young males start to learn song close to the time when they reach independence, and it is likely that in some cases they might be separated from their father [13]. In the wild, juvenile finches form same-age groups after independence [13]. Depending on the environmental conditions, nomadic movements have been observed and song sharing could facilitate group synchronisation and organization as already shown for other species of social songbirds including starlings [20]. In starlings, fledglings tend to stay in juvenile flocks for a least several months and preferentially segregate from adults in roosts and feeding areas [21]. Moreover, when young captive male starlings were housed with peers and only one adult (more young than adult partners), they shared songs preferentially with their same-aged conspecifics [22]. Also, in a study on song sparrows (*Melospiza melodia*), young males developed social relationships with other juvenile males [23]. The authors of the latter study suggest that these associations might facilitate song learning and help young song sparrows to learn the appropriate neighbourhood-specific song types and therefore to take over old territories or to establish new territories. Taken together with the above mentioned work on starlings, our results on the similarly non-territorial colonial zebra finch suggest that imitation between peers in species capable of vocal learning may represent a more widespread phenomenon than generally appreciated.

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Figure legends

Figure 1. Spectrograms of song imitations. A. Best imitation of the father’s song. B. Worst imitation of the father’s song.

Figure 2. Percentage of similarity between song motifs. A. Between the father and its two sons. B. Between son#1 (exposed to the father during the sensitive period) and respectively its father and its brother. C. Between son#2 (never exposed to the father’s song) and respectively its father and its brother.