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1 **Horizontal transmission of the father's song in the Zebra Finch**

2 **(*Taeniopygia guttata*)**

3
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14
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16
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18
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24 **Abstract**

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

36

37 **1. Introduction**

38 Socially meaningful interactions between juvenile animals are an everyday occurrence. In
39 humans, research has shown that infants treat peers as social partners [1]. Juvenile stages are
40 characterized by intense learning, and language acquisition has received particular emphasis
41 [2]. Although language is unique to humans, one of its main components – vocal production
42 learning – is shared with a few animal species. Prominent among these, oscine songbirds learn
43 their species-specific song patterns by memorizing and imitating the songs of adult
44 conspecifics. Some songbird species learn their song during a sensitive period early in life
45 (age-limited learners) while others can learn throughout life (open-ended learners, [3]). The
46 sensitive period of song learning is composed of two phases: a sensory phase and a
47 sensorimotor phase. During the sensory phase, the bird memorizes the acoustic characteristics
48 of the song model; during the sensorimotor phase, the bird uses this auditory memory as a
49 template with which to compare auditory feedback from its own song during the imitative
50 learning process [2,3]. Although young birds learn most of their vocalisations from adults,
51 there is evidence - both from the field and the laboratory - that they can learn from conspecific
52 peers as well [4-6]. In most species studied so far, depriving juveniles of adult song leads to
53 abnormal song development [3]. If a young male zebra finch (*Taeniopygia guttata*) is raised
54 alone with its father, it will develop a song that is a close copy of the paternal song [7,8].
55 However, in the absence of an adult model, untutored juvenile male zebra finches raised in a
56 group will learn song from each other. Indeed, even in the presence of an adult male, juveniles
57 can influence each other's song development. The more male siblings there are in a clutch, the
58 shorter the mean duration of their song motifs and the fewer of their fathers' syllables they
59 imitate, revealing a fraternal inhibition of imitation of the father's song [7]. When young
60 zebra finches can interact freely with peers and adults, juveniles that associate most closely
61 present common song elements [9]. Similarly, in starlings (*Sturnus vulgaris*) juveniles are

62 much less likely to copy adult songs in the presence of peers [10]. These studies suggest that
63 peer experience can affect song learning from adult models. In the present study, we further
64 explore the relative influence of adult and juvenile models by asking whether a young bird,
65 exposed to the song of its father during the early phase of the sensitive period, could lead one
66 of its brothers to imitate the paternal song.

67

68 **2. Material and methods**

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

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

84 Adult male zebra finches produce a 0.5-1.5-s song motif that is repeated several times during a bout of singing
85 (Fig. 1; [13]). The motif is composed of a few syllables repeated in a fixed order. Syllables are highly
86 stereotyped and often contain a combination of different sounds, usually called notes, with fast transitions (on a
87 10-ms timescale). Song of each individual bird was recorded using the Sound Analysis Pro software (SAP 2.062;
88 freely available at <http://soundanalysispro.com/>). The program was run on a PC equipped with an Edirol
89 UA1000 sound card (16 bits, 44.1 kHz), connected to multidirectional Earthworks TC20 microphones (one per
90 sound-attenuating box) placed above the cage. Files containing song phrases were detected using Sound Explorer

91 (developed by R. Jansen, Univ. Amsterdam) and song motifs selected for each bird. We measured similarity
92 between song motifs using an automated procedure implemented in SAP that parametrically quantifies the
93 similarity between songs [14]. This quantification is based on five acoustic parameters: pitch, frequency
94 modulation, amplitude modulation, goodness of pitch and Wiener entropy. Based on these features, the
95 procedure detects similar sections between songs automatically. Using the batch module of SAP, we computed
96 100 comparisons for each triad (father and sons). More details about the sound analysis are provided as
97 electronic supplementary information. Raw data are available at doi:10.5061/dryad.7137r

98

99 **3. Results**

100 In many cases, we found clear evidence of a father's song syllables in the song of the son that
101 was never exposed to him during the sensitive period ("son # 2"; Fig. 1). Therefore, this son
102 learned these sounds by imitating the brother ("son # 1") that was raised with the father from
103 35-42 dph. The son that was exposed to the father produced a better copy of the paternal song
104 than its brother (Fig. 2, Wilcoxon, $p= 0.027$). Nevertheless, its song was more similar to the
105 song of its brother than to the song of their father ($p= 0.02$). Similarly, the song of the
106 unexposed brother was more similar to the song of its brother than to the song of their father
107 ($p= 0.004$).

108 We also observed that the more the exposed juveniles learned from their father, the higher the
109 similarity was between their brother's (who never had contact with the father during the
110 sensitive period) and their father's songs, although this trend was not significant (Spearman,
111 $Rho= 0.57$, $p= 0.12$).

112

113 **4. Discussion**

114 This study shows that a young songbird exposed to its father during the early phase of the
115 sensitive period can lead one of its siblings raised in isolation to imitate the paternal song. We
116 observed a huge inter-individual variability in the number of sounds copied from the father's
117 song, even among sons that were directly exposed to the father during the sensitive period

118 (“son #1”). Moreover, in many cases, songs produced by the two brothers exhibited more
119 similarity to each other than to father’s song.

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

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

137 We observed a huge inter-individual variability in the success of the imitation of the adult
138 model, namely the father’s song. We chose to use sibling pairs and to raise one of them with
139 the father, expecting that vocal sharing would be facilitated between kin for social reasons and
140 not necessarily for genetic reasons since it has been shown that classical song features such as
141 song length or repertoire size exhibit very low heritabilities [17]. Although vocal sharing was
142 high between the two brothers, learning from the father was never perfect, often incomplete

143 and in a few cases almost absent. There are several potential explanations for this result. First,
144 the father did not feed its chicks after 14 dph. Since Immelmann's pioneering studies in this
145 area [18], it has been assumed that one of the most important factors in the selection of a
146 zebra finch song model is the close interaction between a young male and the male that rears
147 it, generally its father. Second, one week of exposure might be insufficient to induce the
148 close-to-perfect vocal imitation that is observed in most cases in which a young bird is raised
149 with an adult until adulthood [8]. Nevertheless, it is known that short exposure to song models
150 is sufficient to induce significant learning in oscine songbirds [3] including zebra finches [19].
151 Third, the relationship developed between the two siblings might have overridden learning
152 from the father for the son that was exposed to him from 35-42 dph.

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

168 work on starlings, our results on the similarly non-territorial colonial zebra finch suggest that
169 imitation between peers in species capable of vocal learning may represent a more widespread
170 phenomenon than generally appreciated.

171

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177

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239 **Figure legends**

240 **Figure 1.** Spectrograms of song imitations. A. Best imitation of the father's song. B. Worst
241 imitation of the father's song.

242

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