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Technological advances for getting insight into the learning capacities of birds in the vocal domain

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1 **Technological advances for gaining insight into the learning capacities of birds in the**
2 **vocal and auditory domains**

3

4 Abstract: Birds produce different types of sounds in different contexts such as begging for
5 food in youngsters, alerting to a danger, defending a territory or attracting a sexual partner.

6 About half of the bird species are able to transform their vocalizations through imitation,
7 improvisation or invention of sounds. Here we review the different experimental procedures
8 that have been used to study the learning capacities of birds in the vocal domain and in the
9 auditory domain, with a particular emphasis on recent technological developments.

10 Nowadays, it is possible to record individual vocalizations of birds living in social groups or
11 to record continuously the vocal ontogeny of birdsong. In conditioning experiments, new
12 paradigms have successfully replaced food rewards with a socio-sexual reward. It is possible
13 to engage in vocal interactions with a bird using dedicated computer systems. In both the
14 laboratory and more recently in the field, different techniques have been used to train young
15 oscine songbirds to learn from acoustic models. The use of virtual social environments and
16 robots as social agents are also promising avenues. All together, these new techniques will
17 permit researchers to explore more deeply the umwelt of bird species.

18

19 **1. Introduction**

20 Birds have fascinated and inspired humans for centuries. Of particular interest have been
21 oscine songbirds (belonging to the suborder Passeri of the perching birds, Passeriformes) that
22 have historically been raised by humans, primarily for aesthetics reasons linked to their
23 plumage and their natural song. But humans have also tried to educate them to produce
24 human words and musical melodies. For example, wind instruments such as “flageolets”
25 (woodwind instruments and members of the fipple flute family) and “serinettes” (‘serin’ is
26 French for canary - a music box similar to a little barrel organ) were used to play tunes to
27 birds to stimulate or train them to sing. These practices were very popular in Europe in the
28 aristocratic milieu in the 18th and the 19th centuries. They took place in the context of
29 conquering, taming and domesticating nature, and to some extent to "civilize" the animals but
30 also to fuel the debate regarding the role of education on human nature (Clouzot & Kreutzer,
31 2019). Breeders of the past, especially from the 15th to the 18th centuries, discovered that
32 innate predispositions to learn can be manipulated through an acute control of social factors
33 during particular moments of the bird’s life (Canary *Serinus canaria*: Hervieux de
34 Chanteloup, 1709; Nightingale *Luscinia megarhynchos*: de Nobleville, 1751, see also the
35 contribution of Baron Von Perneau: Stresemann, 1947; see Birkhead & Van Balen, 2008 for a
36 review). From these reports, we learned that: (1) birds need to be isolated from conspecifics
37 during the vocal practice of these musical melodies but not necessarily during exposure and
38 (2) there is no need to overexpose the birds to the models to imitate: few lessons a day are
39 good enough to trigger good imitations. These results were later confirmed using experiments
40 in the controlled conditions of the laboratory (Thorpe, 1958; Tchernichovski et al., 1999).

41 Particularly during the 18th century, several species were captured in the wild and bred in
42 captivity. Through several different and successive selection processes, wild caged birds of
43 some species then became domesticated ‘cage birds’. Breeders developed techniques to raise

44 and to teach these birds some sounds far removed from their usual vocalizations, taking
45 advantage of vocal production learning. Such learning is also an important component of
46 language, particularly with respect to the ability to imitate environmental sounds especially
47 conspecific ones, an ability exhibited by few taxonomic groups of birds (oscine songbirds,
48 hummingbirds and parrots) and of mammals (whales, bats, seals, elephants and humans) but
49 not in monkeys and apes (Petkov & Jarvis, 2012). Nevertheless, the traditional dichotomy
50 between vocal learners and non-vocal learners seems obsolete since several cases of social
51 influences on some aspects of vocal development have been reported in some species of birds
52 or primates traditionally classified as non-vocal learners (see Watson et al., 2015; Desmedt et
53 al., 2020; Kroodsma et al., 2013 for example). A continuum with respect to graded vocal
54 control seems a more appropriate description nowadays (Petkov & Jarvis, 2012; Tyack, 2020;
55 ten Cate, 2021).

56 Since the invention of the sound spectrograph, birdsong became a useful model system to
57 investigate how experience and genetically determined circuitry interact to shape a learned
58 behavior (Mets & Brainard, 2019) and thousands of birds from tens of species have been
59 raised in controlled conditions of the laboratory to determine how their social environment,
60 and especially their auditory experience, shape their vocalizations. Birdsong acquisition
61 exhibits many similarities with speech and language development (Bolhuis & Everaert, 2013;
62 Marler, 1970; Doupe & Kuhl, 1999; Hyland Bruno et al., 2021; Lipkind et al., 2020).
63 Birdsong learning is based on an auditory-vocal integration: song models heard during a
64 sensory phase are compared to the bird's own vocalizations during the sensorimotor phase
65 when intense practice occurs (Konishi, 1965). As in human infants, vocal developmental
66 learning goes through different stages in juvenile oscine songbirds: following the first weeks
67 of avian babbling, plastic versions of the future song notes and syllables (a terminology
68 inherited from studies on language and music and attested in Medieval and Modern

69 encyclopedias: Fritz, 2016) appear before a process of stabilization called “crystallization”
70 (Thorpe, 1958). From these studies, it was discovered that some species can learn to imitate a
71 unique song during a short sensitive period of early life (“age-limited learners”) whereas
72 others can learn to modify their vocal repertoire during their whole life (“open-ended
73 learners”). It was also discovered that some species do not need to be exposed for weeks to
74 models and can modify their vocalizations through imitation almost immediately (Balsby &
75 Bradbury, 2009). For a long time, it was believed that oscine songbirds could not learn
76 beyond the sensitive period. But successive studies have shown that song learning could still
77 occur in young birds raised in social isolation or exposed to inappropriate models such as
78 tape-recorded songs during the so-called sensitive period before being exposed to an
79 appropriate model. For example, Baptista and Petrinovitch (1984) demonstrated that young
80 white-crowned sparrows (*Zonotrichia leucophrys*) could learn songs after the end of the
81 sensitive period if they were exposed to live tutors but not if they were exposed to taped
82 songs. Most of these studies, done in the laboratory and/or with data collected in the field,
83 provided insight into the processes of song learning, and more generally of vocal learning, in
84 a more relevant context (Carouso-Peck et al., 2021).

85 Significant knowledge has been gained on the sensorimotor aspects of vocal production and
86 learning these last 25 years with the development of computers and software. Here we present
87 these different improvements for different purposes linked to learning in the vocal domain
88 such as vocal recording and analysis, song tutoring, conditioning experiments and controlled
89 vocal interactions. Even if most research deals with birdsong learning in oscine songbirds, our
90 review is not restricted to vocal production learning capacities and could embrace other types
91 of learning in the vocal domain such as contextual learning (Janik & Slater, 1997) that could
92 be applied to a wide range of bird species including species traditionally classified as non-

93 vocal-learners. We will conclude by suggesting potential lines of research on the use of
94 computers in the field of avian communication that seem feasible in the future.

95

96

97 **2. Continuous vocal recording and analysis: from a single individual to group members**

98 Before the age of computer technology, sound recordings were saved on tapes which
99 drastically limited quantitative accumulation and analysis of data. It is also worth noting that
100 the Kay Sona-Graph (which was also prohibitively expensive for many researchers) could not
101 display a sonogram representing more than 1.5sec of sound, which for a long time restricted
102 birdsong research to short vocalizations and thus often to songs of only a few species. A
103 major step was reached when vocal recording and analysis were completely digitalized
104 (Tchernichovski et al., 2004; Gardner et al., 2005). Such continuous recording and analysis
105 permitted, for example, the discovery of the role of sleep on developmental song learning
106 (Derégnaucourt et al., 2005; Shank & Margoliash, 2009), the role of melatonin on vocal
107 production and learning in both vocal and non-vocal learners (Derégnaucourt et al., 2012) and
108 the ability to track cultural evolution of birdsong in the laboratory (Fehér et al., 2009). Such
109 methods also allowed the exploration of vocal ontogeny in both vocal and non-vocal learner
110 species (Gardner et al., 2005; Derégnaucourt et al., 2009) and the discovery of some vocal
111 changes that would have been unnoticed without continuous recording. Such systems were
112 developed to record a bird kept singly in a sound-proof chamber, and to analyze the sound
113 recorded online, which also permitted researchers to detect vocalizations and to discard cage
114 noises. The invention of spectrographic analysis also allowed researchers to focus on the
115 accuracy of imitation during vocal learning. Initially, imitation was determined by researchers
116 eyeballing spectrograms with some issues on inter-observer reliabilities depending on their

117 experience (Jones et al., 2001). Some progress has been made by automatizing digital
118 similarity measurements between different sounds, e.g., between a tutor's song and its
119 imitation by a pupil (Tchernichovski et al., 2000; Lachlan et al., 2010). Such an approach
120 depends on specific song features selected by experimenters. In a more recent attempt, Mets
121 and Brainard (2018) used a statistical model to broadly capture the structure of each song, and
122 then estimated the divergence between the model and its imitation. The authors emphasized
123 that this measure could be used to quantify changes in other behaviors such as human speech
124 (Mets & Brainard, 2018). Continuous recordings at the group level is now permitted thanks to
125 the development lightweight wireless microphone backpacks (Anisimov et al., 2014; Gill et
126 al., 2016). These methods allow birds to behave freely in a social group and enable studies of
127 vocal interactions. For example, Gill et al. (2015) observed that call occurrences and
128 repertoire changed over the breeding cycle in a group of zebra finches (*Taeniopygia guttata*).
129 In another study, simultaneous recordings of individual vocalizations and multiunit vocal
130 premotor activity in breeding pairs of white-browed sparrow-weaver (*P. mahali*) ranging
131 freely in their natural habitat permitted researchers to document how the precise inter-
132 individual coordination of motor activity during duet singing is neuronally controlled
133 (Hoffman et al., 2019). The authors observed that rhythmic social interactions that require
134 temporal coordination are not just associated with a coherent oscillation of activity in large
135 areas of both interacting partners' brains but with an inter-individually synchronized
136 activation of small groups of neurons within the same brain nucleus in both partners. Again,
137 such study would have not been possible without continuous recording. In the field,
138 microphone arrays are also increasingly used to remotely monitor acoustically active animals
139 including birds (Blumstein et al., 2011) but to our knowledge, they had never been used to
140 study directly the learning capacities of birds in the vocal domain even if changes in the

141 soundscape tracked by studies in the field of eco-acoustics (Stowell & Sueur, 2020) might
142 capture these aspects.

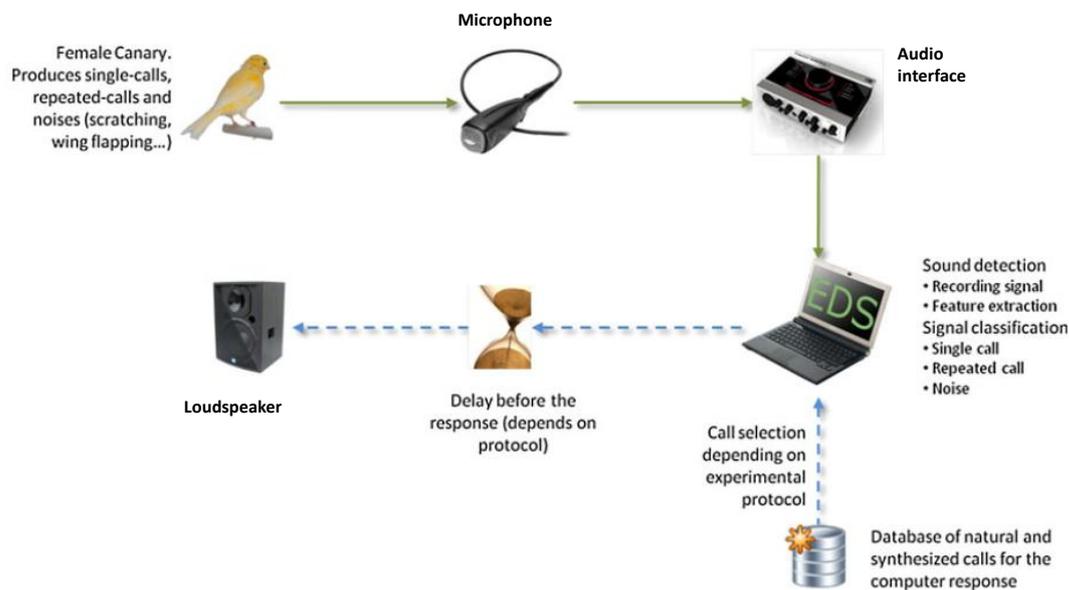
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144 **3. Controlled vocal interactions**

145 As mentioned above, continuous recordings permitted researchers to document vocal
146 interactions between two individuals and at the group level. This necessitates automatic
147 detection of sounds and adapted response with the possibility to accurately control the delay
148 between sound detection and response. Turn-taking is an important component of language
149 and has been demonstrated in early infancy in humans and also in other species (Levinson,
150 2016). Such a process has also been the subject of much research in birds, especially in the
151 context of territory defense in oscine songbirds and has been simulated using interactive
152 playback (Slater et al., 2003). For example, song type matching is found in some species such
153 as the song sparrow (*Melospiza melodia*; Akçay et al., 2013; Beecher et al., 2000). It has been
154 observed that birds approached a type-matching stimulus much more aggressively than a non-
155 matching stimulus (Vehrencamp, 2001). Using a call detector implemented into an automated
156 playback paradigm, Okanoya and Kimura (1993) observed that Bengalese finches (*Lonchura*
157 *striata*) responded only to the Bengalese finch calls, but not the zebra finch calls, and female
158 calls were more efficient in inducing responses than male calls. Using a dedicated software
159 that permits continuous recording and real-time analysis, and a plastic model of a zebra finch
160 equipped with a speaker, Benichov and colleagues (2016) investigated the neurobiological
161 basis of turn-taking in zebra finches. Using an isochronous call pattern (e.g. one call per
162 second), they observed that finches adjusted their call timing rapidly. Then, they changed the
163 timing to enhance jamming, namely to increase the probability to overlap the birds' calls with
164 calls sent by the system. All zebra finches adjusted their call pattern to avoid jamming, either
165 by calling earlier, later or both. When the experimenters used a pattern of alternating single

166 and paired calls, finches adjusted the timing of their calls differently for the single compared
 167 to the paired calls. Interestingly, females performed better than males at these tasks. The
 168 authors observed that fully functional forebrain regions, part of the so-called “song control
 169 system” – a set of several brain nuclei involved in song production, perception and learning -
 170 are necessary for this precise timing in both males and females (Benichov et al., 2016).

171 Such a close-loop computer system was also used successfully in domestic canaries to
 172 investigate the functions and context of production of two types of calls: “single calls” and
 173 “repeated calls” (Figure 1, Lerch et al., 2011).



174

175 *Figure 1. Scheme of the closed-loop interaction between a canary and the computer system.*
 176 *Solid green arrows indicate the flow of acoustic signals produced by the bird. Dashed blue*
 177 *arrows indicate the signal produced by the system as a response to the bird’s vocalization.*
 178 *Modified from Lerch et al., Animal Cognition, 2011.*

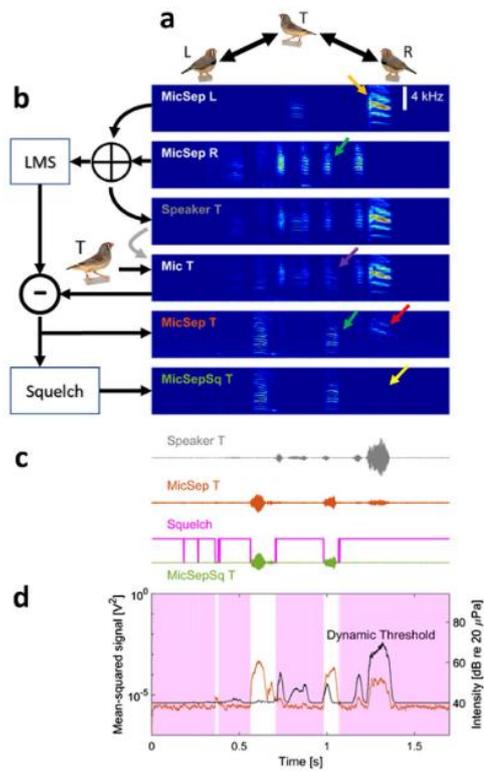
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180 The experimental procedures involved different stimuli (either natural or artificially
 181 synthesized) and different scenarios (e.g. positive interaction: the computer responded with a

182 single call when the bird produced a single call and with a repeated call when the bird
183 produced a repeated call, and negative interaction: the computer responded with a single call
184 when the bird produced a repeated call, and with a repeated call when the bird produced a
185 single call). Only females were tested: they produced significantly more single than repeated
186 calls (either in response to natural and synthesized calls), and their rate of single calls was
187 associated with the context (more often higher in the case of positive interaction), whereas
188 repeated calls were context independent. This experiment confirmed a long-term assumption
189 that “single calls” act as contact calls in canaries, whereas “repeated calls” are mostly used in
190 a context of stress (Mulligan & Olsen, 1969).

191 More recently, Rychen and colleagues (2021) developed a system for real-time control of
192 vocal interactions among separately housed animals. The system is implemented on a Field-
193 Programmable Gate Array (FPGA) and it can control communication networks by restricting
194 vocal exchanges among chosen individuals up to four animals (Figure 2). For example, an
195 individual could interact with other individuals that could not hear each other. Such system
196 also gives the possibility to mimic eavesdropping situations when one individual can listen to
197 vocal exchanges between other individuals without being noticed by the others.

198



200

201 *Figure 2. System controlling vocal communication networks. (a) The female T on top is*
 202 *bidirectionally connected (arrows) with two males L and R that are not supposed to hear each*
 203 *other (hierarchical network). (b–d) Example in which T and L call simultaneously (green*
 204 *arrows). (b) Even though Mic T records a superposition of both calls (magenta arrow), L's*
 205 *call gets cleanly filtered out (MicSep T) by the LMS (Least Mean Squares) filter. In contrast,*
 206 *a louder call by L (orange arrow) leaves a significant echo on MicSep T (red arrow). The*
 207 *squelch (an algorithm that prevents transitive sound propagation in linked chambers for*
 208 *example here bird L cannot hear bird R) removes the residual of that call on MicSepSq T*
 209 *(yellow arrow), which constitutes a clean signal, just as if L had been silent. Spectrograms*
 210 *have been normalized to individual color scales. (c) Shown are the Speaker T (gray), MicSep*
 211 *T (red), and MicSepSq T (green) sound waveforms. (d) The light magenta regions indicate*
 212 *times when the squelch is active and signal transmission is blocked. Modified from Rychen et*
 213 *al. Scientific Reports 2021.*

214 **4. Enhancing song tutoring**

215 In the study of song ontogeny, there have been methodological advances and improvements
216 since the early days of simple playback of taped songs. This includes control of song playback
217 by subject, playback augmented by visual stimuli, playback of vocal interactions and more
218 recently the development of robots as song tutors.

219

220 4.1. Song playback

221 Different artificial methods have been developed in the laboratory to train young birds to
222 learn songs. Since the pioneering works of Peter Marler using tape playback to train young
223 sparrows to learn a song (Marler, 1970; Marler & Peters, 1977), tens of species have been
224 exposed to their specific songs or other models during the sensitive period with mixed results:
225 if some species do learn pretty well using such a passive exposure, some do not (e.g., Zebra
226 Finch; Derégnaucourt et al., 2013). In this species, when song presentation was made
227 contingent upon key pressing, young males copied to a greater extent than controls receiving
228 the same stimulation in a passive way (Adret, 1993a) and the effectiveness of the contingency
229 for initiating song imitation was greater for key pressing rather than hopping on a reinforcing
230 perch (Adret, 1993b, but see James & Sakata, 2017). As previously mentioned, few daily
231 exposure of song models are sufficient to trigger good learning (Tchernichovski et al., 1999;
232 Deshpande et al., 2014). Using this paradigm and other experimental and computational
233 approaches to manipulate and analyze the birds' vocal development, several studies have
234 revealed different rules during birdsong developmental learning that exhibit analogies with
235 language acquisition in humans (Lipkind et al., 2013, 2017, 2020; James & Sakata, 2017;
236 Mets & Brainard, 2018).

237 For example, zebra finches could be exposed to non-conspecific songs as models such as
238 heterospecific sounds (Gehrold et al., 2013) and canaries to synthetic sounds (Gardner et al.,
239 2005). It was observed that this ability to learn non-conspecific songs is restricted to the
240 production of avian babbling and does not persist into adulthood (Gardner et al., 2005). In
241 another experiment, young male zebra finches were exposed to synthesized songs consisting
242 of five species-typical syllables arranged in every possible five-syllable sequence (n = 120
243 possible sequences) (James & Sakata, 2017). The authors observed that all birds converged
244 towards similar song sequences showing that there exist learning biases underlying song
245 organization in this species. Dina Lipkind and colleagues have used extensively a paradigm
246 that consists of switching song models during the sensitive period for song learning to study
247 how young birds cope with vocal changes both in the temporal and the spectral domains
248 during ontogeny (Lipkind et al., 2013, 2017, 2020). For example, young finches were exposed
249 to a song model composed of three syllables (A-B-C) and when they started to produce the
250 right sequence, they were exposed to another song model with the same syllables in a
251 different order (A-C-B). Some birds succeeded to modified their song but after a huge
252 practice involving their learning of new syllable transitions such as A to C and C to B
253 (Lipkind et al., 2013). Such vocal changes imposed experimentally in birds exhibit analogies
254 with language acquisition in humans (Lipkind et al., 2013). The study of interactions between
255 genetic predispositions and experience is a huge topic in ethology and in birdsong research in
256 particular. In a series of experiments with Bengalese finches, Mets and Brainard used both
257 cross-fostering and computerized instruction with synthetic songs to demonstrate that
258 matching the tutor song to individual predispositions can improve learning across genetic
259 backgrounds (2019). All together, these examples show how being able to manipulate sound
260 playback to birds during song ontogeny could shed lights on general mechanisms of learning.

261 In the field, experimental evidence of birdsong learning was demonstrated recently in wild
262 savannah sparrows (*Passerculus sandwichensis*, Mennil et al., 2018). The authors used an
263 array of loudspeakers to broadcast conspecific songs recorded in North America to birds
264 living on an island. They also observed that these new songs spread in the subsequent
265 generations.

266

267

268 4.2. Influence of visual stimuli

269 Several experiments have shown that birdsong acquisition is not an auditory phenomenon per
270 se and that multimodal cues are also involved in the learning process, including visual stimuli.
271 Their influence on birdsong learning was demonstrated for example in nightingales: song
272 acquisition was enhanced when playback was associated with strobe light produced
273 synchronously with the temporal and amplitude patterns of the song models (Hultsch et al.,
274 1999). Several experiments used visual stimuli combined with audio playback including
275 taxidermic mounts or plastic dummies (see Derégnaucourt, 2010 for a review). Adret (1997)
276 trained finches to peck a key to trigger a video movie and observed poor learning. This result
277 could be explained by the flickering frequency of Cathode Ray Tube (CRT) used for this
278 experiment, that exhibited a time resolution too low for birds. TFT (Thin Film Transistors)
279 have been used successfully to induce behavioral reactions in birds (e.g. courtship songs in
280 zebra finches and Bengalese finches: Ikebuchi & Okanoya, 1999) and for the purpose of song
281 tutoring, even if, to our knowledge, there have been only a couple of studies dealing with
282 these aspects that have been published and presented below. In an experiment in zebra
283 finches, Deshpande et al. (2014) used different paradigms during a sole day of training (20
284 key pecks allowed): following a key-peck as described above, the audio-visual components of

285 song models were played either simultaneously (Sim) or in a staggered fashion where birds
286 received either audio before video (AV) or video before audio (VA). When trained at 45 dph
287 (day post-hatch), AV and Sim groups showed significantly higher similarity to the song
288 model than did an untrained group of birds kept in social isolation during the sensitive period.
289 However, there were no significant differences between the different groups of trained birds.
290 By contrast, when trained at 35 dph, differences in the efficacy of these audio-visual training
291 stimuli became apparent. Surprisingly, a single training session at this age was effective only
292 in the AV condition. This result is reminiscent of the Colavita visual dominance effect
293 (Colavita, 1974): when one has to respond simultaneously to an auditory signal and to a visual
294 signal, one tends to respond only to the visual signal which illustrates visual dominance in
295 attentional processes. But as mentioned by the authors, further work is required to explore
296 these aspects.

297 In a recent experiment, dyads consisting of a young male and an unrelated young female were
298 exposed passively to audio-video recordings of a singing adult male. If birds approached the
299 setup more often and spent more time close to it than juveniles exposed to audio playback
300 only or audio playback combined with pixelated and time-reversed videos, they did not
301 exhibit better imitation of the tutor song (Varkevisser et al., 2021).

302

303 4.3. Playback of vocal interactions

304 Several studies suggest that listening to vocal interactions between adults or between an adult
305 and a young could enhance vocal learning. Such paradigm, inspired by the seminal work of
306 Dietmar Todt (Model/rival approach; Todt, 1975) has been used with success by Irene
307 Pepperberg to train Alex and other grey parrots (*Psittacus erithacus*) to learn human words
308 and to associate them with different types of objects (social modeling theory, Pepperberg,

309 1985). In this context, parrots could observe interactions between two humans, one person
310 being the ‘trainer’ and one being the ‘model’ as well as the ‘rival.’(Pepperberg, 1985). Young
311 European starlings (*Sturnus vulgaris*) raised in social isolation learned better when they could
312 hear live interactions than while exposed to playback of taped songs (Poirier et al., 2004). In
313 another experiment with song sparrows (*Melospiza melodia*), hand-raised birds were exposed
314 sequentially to two pairs of adult males in Summer (Burt et al., 2007). During the first three
315 months of the next year, a computer program was used to simulate a live, interactive tutor.
316 Individuals were exposed to computer presentations of songs from two of the original live
317 tutors: one of the two “virtual” tutors sang interactively with the young bird while the other
318 sang asynchronously. The song classifier program used a spectrograph cross-correlation
319 algorithm to compare the detected subject’s song against examples from the tutor’s repertoire.
320 The classifier returned a score indicating the similarity of the detected subject song to each of
321 the tutor examples. If the score of the most similar tutor example type was above a fixed
322 threshold, then the virtual tutor concluded that the subject had sung that type, otherwise it
323 considered the subject had sung an unknown type. The virtual tutor then acted upon this
324 information. The classifier parameters and similarity threshold were calibrated a priori using a
325 test set of different song sparrow songs and the classifier output was periodically assessed
326 during tutoring to verify that it was working reasonably (Burt et al., 2007). Subjects learned
327 relatively more from their interactive tutor and his early partner than from the non-interactive
328 one (Burt et al., 2007). More recently, it has been shown that wild savannah sparrows can
329 learn novel songs broadcast by speakers but that songs broadcast in a simulated
330 countersinging context were not better learned than songs broadcast by speakers simulating
331 solo singing (Mennil et al., 2019). To perform this experiment, the authors created playback
332 stimuli by assembling tutor songs into stereo playback tracks. Each track featured two

333 simulated tutors engaged in simultaneous bouts of interactive singing, or in alternating bouts
334 of non-interactive singing.

335

336 4.4. Towards an integrative approach to study the influence of multimodality: use of robots

337 As mentioned above, birdsong learning is a multimodal task involving behavioral contingency
338 and several studies have emphasized that a live tutor could be better than taped playback or a
339 computer to train a bird to imitate songs (Baptista & Petrinovitch, 1986; Derégnaucourt et al.,
340 2013). More recently, Mets and Brainard (2018b) demonstrated that increasing the richness of
341 the learning experience from poor (tutoring by computer) to a richer level of interactions
342 (tutoring by a live bird) reduces the genetic influence in favor of experiential influence in
343 Bengalese finches. Experiments involving a human tutor are the most emblematic to illustrate
344 this phenomenon, e.g. those of Jürgen Nicolai training bullfinches to imitate whistled
345 melodies (Nicolai et al., 2014). To study the multimodal aspects of song tutoring, one should
346 be able to handle each behaviour of the tutor independently, and assess the impact of each
347 stimulus not only on the establishment and maintenance of the relationship between the young
348 bird and the adult bird, but also on the success of song imitation. There is a growing interest
349 for the use of robots in ethology (see Romano et al., 2019 for a review) and ethorobotics -
350 even if it is primarily focused on human-robot relationships - is a fast-growing discipline. For
351 example, in birds, robots were used successfully to study courtship behaviour in bowerbirds
352 (Patricelli et al., 2002, 2006; Perry et al., 2019), filial imprinting in juveniles quails (Jolly et
353 al., 2016), collective and social behaviour in chickens (Gribovskiy et al., 2018) and public
354 information in starlings (Butler & Fernández-Juricic, 2014). We recently developed a robotic
355 zebra finch that we used as a song tutor for young finches. The robot is that of a life-sized
356 zebra finch and is painted to represent an adult male; it is fixed on an axis and can move
357 different parts of its plastic body. It can be programmed to behave contingently: for example,

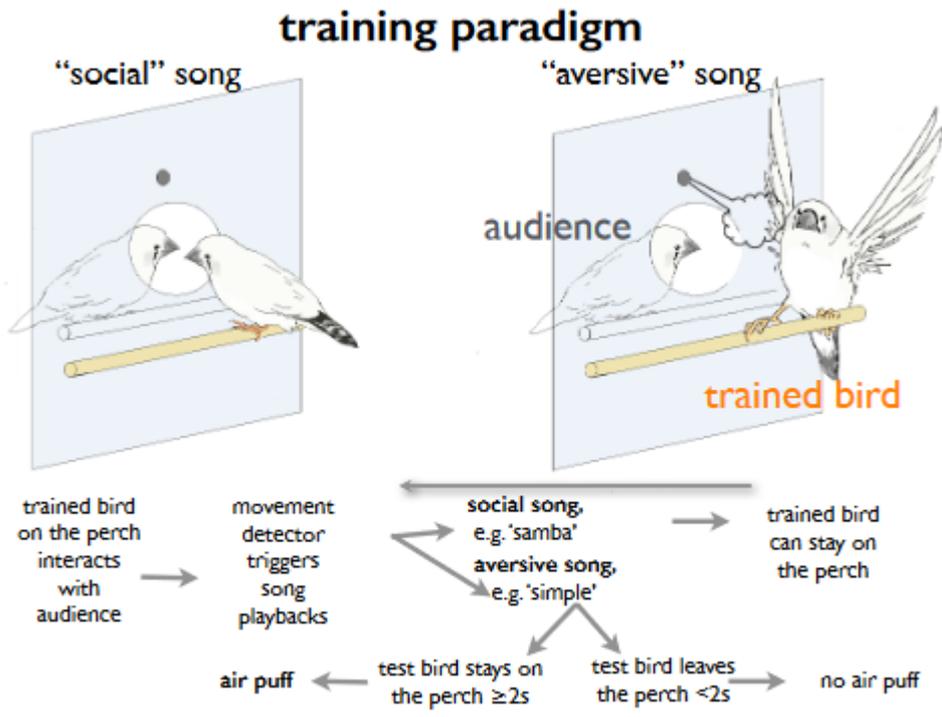
358 when the young bird sits on a perch close to it, it moves towards him and sings. The program
359 is also implemented with a vocal loop (see above): when the bird produces a contact call, the
360 robot replied with a contact call and it is possible to manipulate the latency of the response.
361 Using such a contingent program, we observed that young finches exposed to a robot one
362 hour a day for five days a week during five weeks provided a good imitation of the song
363 model. We did not find a significant difference in song imitation between birds tutored with a
364 robot and birds tutored by a live male (Araguas et al., 2022), this latter condition being known
365 until now as the best way so far to get a close-to-perfect imitation of a song model in zebra
366 finches (Tchernichovski et al., 1999; Derégnaucourt et al., 2013).

367

368

369 **5. Conditioning experiments**

370 The usual paradigm used in conditioning experiments consists in providing a reward for good
371 responses (e.g. food) and a penalty for bad responses (lights off or electric shock). In go-no go
372 procedures, animals are usually food-restricted to make sure that they would be motivated to
373 peck on keys or press on levers to participate in experiments. Recently, new techniques have
374 been developed by taking into account the socio-sexual tendencies of zebra finches. In these
375 scenarios, finches do not work for food but to see and/or interact vocally with conspecifics.
376 For example, Tokarev and Tchernichovski (2014) developed a new design to measure
377 auditory discrimination (Figure 3).



378

379 *Figure 3. Social reinforcement apparatus: playbacks of the 'social' song allow birds to*
 380 *socialize via a window; playbacks of the 'aversive' song are followed by an air puff, which*
 381 *the bird learns to avoid. Artwork courtesy of Lotem Tchernichovski. Source: Tokarev and*
 382 *Tchernichovski, BioRxiv : 004176, 2014.*

383

384 A male is allowed to interact with a female while perching next to a small window. Playbacks
 385 of one syllable were followed by an air puff (aversive syllable), causing the bird to escape to
 386 the safe perch, while playbacks of the other syllable allowed the interaction to continue. Using
 387 this paradigm, it was shown that learning auditory discriminations from observation is
 388 efficient but less robust than learning from experience (Narula et al., 2018). The authors
 389 trained an "experimenter" zebra finch to discriminate between auditory stimuli in the presence
 390 of an "observer" finch. Experimenters were slow to successfully discriminate the stimuli, but
 391 immediately generalize their ability to a new set of similar stimuli. By contrast, observers
 392 subjected to the same task were able to discriminate the initial stimulus set, but require more

393 time for successful generalization (Narula et al., 2018). Taking again into account the natural
394 tendency for isolated finches to seek socio-sexual contacts, Macedo-Lima and Remage-
395 Healey (2020) replaced the food reward by a social reward for an experiment to measure
396 auditory discrimination in zebra finches. A male and a female were put in adjacent cages
397 separated by a sheet of opaque polarized glass. If a GO tone was played, the glass would turn
398 transparent for 6 s, resulting in a HIT (i.e., period of visual engagement with the adjacent
399 social partner through the transparent barrier). The authors did not document whether training
400 was faster with a social reward rather than a food reward but it is likely that a dedicated
401 experiment to test this prediction should be run in order to answer this question.

402

403 **6. Future directions**

404 Birdsong has been established as a biological model of choice to study vocal learning and, as
405 a consequence, the goal of several experimental procedures is to enhance song imitation or
406 even to obtain a perfect copy of the model (Derégnaucourt et al., 2013; Mets and Brainard,
407 2019). The robotic zebra finch, which permits both vocal and behavioural contingencies with
408 a young bird's behaviour, offers new opportunities to reach this goal and to explore
409 meticulously the multimodal cues involved in birdsong learning (Araguas et al., 2022). Such
410 multimodal aspects of communication in birds could also be explored using other computer
411 systems, such as the one recently developed to control vocal exchanges in a group (Rychen et
412 al., 2021); as mentioned by the authors, it would be easy to combine the visual
413 communication channel using cameras and computer screens. Despite the importance of flight
414 in the life of birds, birdsong has mainly been studied in perching birds, and vocal production
415 learning in flight presents unique challenges and opportunities for birds and for researchers
416 (Berg et al., 2019; Arnold et al., 2022). Affordable, high-speed, high-resolution cameras and

417 mic-video array technology now available to tackle a number of questions in spatial and
418 biomechanical issues related to highly mobile communication strategies.

419 Since the pioneering works of Adret (1993a, b) showing that young male zebra finches learn
420 quickly to press a button to trigger song playback, several experiments have highlighted the
421 active role of young songbirds on birdsong learning. Automatic learning devices also have
422 potential to advance the study of social learning. For example, devices such as the one used
423 with monkeys by Fagot and Paleressompoulle (2009) could allow experiments in which birds
424 living in a social group choose when to participate.

425 Experiments involving young birds raised in social isolation during several weeks or months
426 raise ethical issues. In ethology, this experimental procedure is still considered as the baseline
427 reference conditions even if it exhibits several pitfalls already pinpointed a long time ago
428 (Lehrman, 1953). More recently, it has been shown that acute social isolation has immediate
429 consequences on brain gene activity in zebra finches (George et al., 2020). The use of
430 biomimetic robots appear as a promising avenue to fulfill the 3Rs' objectives (Replace,
431 Reduce, Refine: Replacement alternatives refer to methods which avoid or replace the use of
432 animals, reduction alternatives refer to any strategy that will result in fewer animals being
433 used to obtain sufficient data to answer the research question, refinement alternatives refer to
434 the modification of husbandry or experimental procedures to minimize pain and distress and
435 to improve welfare; Bierbach et al., 2021); in birdsong research, robots could replace live
436 companions and therefore potentially reduce the stress of social isolation without
437 compromising highly standardized conditions. Interactions between wild birds and machines
438 open also exciting opportunities of research such as the ability to track cultural evolution of
439 birdsong following the introduction of new song models, but it also raises ethical questions
440 (Mennill et al., 2019). The use of biomimetic robots could also be relevant in the field of
441 biological conservation. For example, a recent study has shown that young regent honeyeaters

442 (*Anthochaera phrygia*) are more likely to learn songs from heterospecific models due to the
443 lack of sufficient conspecific adult tutors (Crates et al., 2021). Robots mimicking conspecific
444 adults could be used for song tutoring and could permit the maintenance of endangered
445 dialects.

446 The use of Virtual Reality (VR) is also a promising avenue to study the learning capacities of
447 birds in the vocal domain, especially in the field of birdsong learning (Ljubičić et al., 2016).
448 For example, birds could be exposed to a Virtual Social Environment (VSE) that simulate the
449 social context of song learning, through iterative interactions between the developing bird and
450 a computerized visual and vocal interface comprising one or several birds (Ljubičić et al.,
451 2016). Such a use is still at its infancy for behavioural studies in non-human animals. Studies
452 on insects have pioneered the implementation of VR paradigms to study perceptual and
453 cognitive capacities (Lafon et al., 2021).

454 In conclusion, our knowledge on learning capacities of birds in the vocal and auditory
455 domains has been rapidly growing these last 20 years thanks to technological developments.
456 Many setups developed recently are based on inexpensive devices and free and open-source
457 softwares. Cloud platforms permit the storage of huge amount of data that can be easily
458 shared and accessed by researchers. Such tools used both in the laboratory and the field will
459 permit researchers to get more insight into the evolutionary processes that led to species
460 differences regarding learning abilities and to explore more deeply the umwelt of birds. These
461 new techniques offer some opportunities to improve our knowledge of birds' behaviour in
462 more natural settings, ultimately improving some ethical aspects of experimental research.

463

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