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**The perception of self in birds**

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10 **Abstract:**

11 The perception of self is an important topic in several disciplines such as ethology,  
12 behavioral ecology, psychology, developmental and cognitive neuroscience. Self-  
13 perception is investigated by experimentally exposing different species of animals to self-  
14 stimuli such as their own image, smell or vocalizations. Here we review more than one  
15 hundred studies using these methods in birds, a taxonomic group that exhibits a rich  
16 diversity regarding ecology and behavior. Exposure to self-image is the main method for  
17 studying self-recognition, while exposing birds to their own smell is generally used for the  
18 investigation of homing or odor-based kin discrimination. Self-produced vocalizations –  
19 especially in oscine songbirds – are used as stimuli for understanding the mechanisms of  
20 vocal coding/decoding both at the neural and at the behavioral levels. With this review, we  
21 highlight the necessity to study the perception of self in animals cross-modally and to  
22 consider the role of experience and development, aspects that can be easily monitored in  
23 captive populations of birds.

24

25 **1. Introduction**

26

27 ***1.1. The Concept of Self: definitions***

28

29 There is a biological necessity for distinguishing self from non-self at various levels of  
30 organization: from physiological processes at the cellular level (e.g. to produce an immune  
31 response) to individual-level behaviors, such as discriminating kin and identifying  
32 conspecific and hetero-specific cues (Sherman et al., 1997). Lewis (1994) proposed a  
33 distinction between two levels of self that are often confused: “the machine self”, the  
34 greater part of the self, which knows without knowing that it knows, and the “idea of me”,  
35 the smaller part – included in the machine self – which knows that it knows. The second  
36 level refers to self-awareness, and involves the idea of consciousness which constitutes the  
37 corner stone of the Theory of Mind (Edelman & Seth, 2009).

38 To better understand the concept of the “machine self”, we can refer to *self-referent*  
39 *phenotype matching*. During its development, an animal learns some aspects of its own  
40 phenotype, in particular through self-directed behaviors, which it later uses as a referent or  
41 template to identify relatives (kin recognition) or conspecifics (species recognition)  
42 (Hauber & Sherman, 2001). Dawkins (1982) euphemistically called it the ‘armpit’ effect.

43 As underlined by Bekoff & Sherman (2004) such self-referencing can be reflexive and  
44 non-cognitive. These authors suggest two other degrees of self-cognizance: (1) self-  
45 awareness, that enables an individual to discriminate consciously or subconsciously  
46 between its own body or possessions from those of others, and (2) self-consciousness,  
47 which involves having a sense of one’s own body as a named self, and thinking about one’s

48 self and one's own behavior in relation to the actions of others. According to Bekoff &  
49 Sherman (2014), self-awareness does not imply that individuals use self-referent  
50 phenotype matching or vice versa, whereas self-consciousness implies that an individual is  
51 self-aware, and that it can use self-referencing. Therefore, self-referent phenotype  
52 matching is probably a prerequisite for self-consciousness. However, other researchers do  
53 not make the same distinction between self-awareness and self-consciousness and these  
54 two expressions are often used with the same significance. For example, Lewis (2011)  
55 defines self-awareness as "a mental representation of me."

56

### 57 ***1.2. Mirror Self-Recognition***

58

59 Several experimental paradigms have been designed to explore these aspects of self-  
60 awareness and self-consciousness in animals. Among them, the mirror mark test,  
61 developed by Gordon Gallup (1970), seeks to determine whether an animal recognizes  
62 itself in the mirror by marking a colored dot on the animal's body. The mark needs to be  
63 placed on an out-of-view body part so that it can be detected only with guidance of a mirror.  
64 This is done without the subject noticing (subjects were often anesthetized for the first  
65 studies) or with a procedure of sham marking used as a control. The mark test determines  
66 if the animal can use its reflection to locate the mark on its body, as measured by its  
67 inspection, touching, or rubbing of the spot. Very few species pass the mark test of mirror  
68 self-recognition (MSR) (Table 1).

69 In humans, MSR does not emerge until 15-24 months of age (Amsterdam, 1972; Lewis,  
70 2011) when the first signs of self-awareness appear: these include introspection and mental

71 state attribution (Piaget, 1952) along with empathy (Bischof-Kohler, 2012), the use of  
72 personal pronouns and pretend play (Lewis & Ramsay, 2004). Apart from humans, strong  
73 evidence of MSR have been obtained only for the four great apes (Anderson & Gallup,  
74 2011), bottlenose dolphins (*Tursiops truncatus*; Reiss & Marino, 2001), Asian elephants  
75 (*Elephas maximus*; Plotnik et al., 2006) and magpies (*Pica pica*; Prior et al., 2008). A  
76 variety of organisms including fishes, birds, sea lions, dogs and cats, although they have  
77 not been formerly tested with the mirror mark test, produce very different behaviors toward  
78 their own reflections (Parker et al., 1994). Several species persist in responding to mirrors  
79 as if confronted by another conspecific, even in the case of years of continuous exposure  
80 to mirrors (Suarez & Gallup, 1986). Mirrors induce socially meaningful and strong  
81 responses with such reliability that mirror-image stimulation has been extensively  
82 employed to study aggressive and social patterns in a wide variety of species from fishes  
83 to mammals (Parker et al., 1994). Some of these species demonstrate the ability to use a  
84 mirror to mediate or guide their behavior, for example macaques (*Macaca fuscata*) can use  
85 a mirror to reach hidden food that is only visible with a mirror (Itakura, 1987). However,  
86 the conclusion that self-directed behavior in response to a mirror implies some form of  
87 human-like self-awareness is not free from controversy (Parker et al., 1994). Similarly,  
88 implication of self-recognition when passing the mark test is also a subject of debate  
89 (Medina et al., 2011; Suddendorf & Butler, 2013).

90 While visual self-stimuli have extensively been used in primates, there is debate as to the  
91 value of tests that rely primarily on senses other than vision. The mirror test has been  
92 adapted to other modalities, such as scent. For instance, Bekoff (2001) developed a  
93 paradigm using urine-saturated snow ('yellow snow') for testing self-awareness in dogs.

94 Besides their own reflection and their own smell, animals have also been exposed to their  
95 own vocalizations, not necessarily in the context of studying self-awareness. Indeed, if self-  
96 recognition is an important topic in comparative psychology or cognitive neuroscience,  
97 exposure to self-stimuli is often used as a control in ethology or behavioral ecology. This  
98 paradigm has been extensively used in bird species in different contexts, which we  
99 summarize in the next section.

100

### 101 ***1.3. Why study the perception of self in birds?***

102

103 The class *Aves* is composed of about 10,000 species with a rich diversity regarding their  
104 ecology and behavior.

105 Several experiments and observations in birds have indirectly shown that the perception of  
106 self is particularly relevant during interactions with other individuals, especially in the  
107 context of sexual selection. Monogamy is particularly widespread in birds and several  
108 species exhibit assortative pairing: pairing with an individual of similar quality or  
109 geographical origin. For example, non-random mating with respect to coloration is  
110 commonly observed in birds (Hill, 2006). In domesticated budgerigars (*Melopsittacus*  
111 *undulatus*), females prefer potential mates with contact calls more similar to their own  
112 (Moravec et al., 2010). In the laboratory, Holveck and Riebel (2009) observed that female  
113 zebra finches (*Taeniopygia guttata*) reared in poor conditions develop acoustic preferences  
114 for the songs of males reared in similar conditions. Several experiments have also shown  
115 that females reduce their choosiness when their body condition is experimentally  
116 compromised (Burley & Foster, 2006; Lerch et al., 2011, 2013). For example, cutting the

117 flight feathers of female canaries (*Serinus canaria*) decreases female choosiness towards  
118 male songs. The authors propose that this decrease in choosiness is likely to be a residual  
119 behavioral adaptation of being in poor conditions and it follows the evaluation of their own  
120 flight quality in the aviary and therefore results from the perception of self-properties  
121 (Lerch et al., 2013).

122 The perception of self can also be affected by the experience of the animals. Some species  
123 have the possibility to modify their self-characteristics through learning, and this is  
124 particularly well-documented in some bird species in the vocal domain (Bolhuis et al.,  
125 2010; Bradbury & Balsby, 2016). Like humans, oscine songbirds, parrots and  
126 hummingbirds exhibit vocal production learning, the capacity to imitate sounds from their  
127 environment, mainly those produced by conspecifics. This ability which is a prerequisite  
128 for the development of human speech, is a rare trait in the animal kingdom and is shared  
129 with certain marine mammals, elephants and bats but seems to be absent in non-human  
130 primates (Bolhuis et al., 2010), although some vocal plasticity and abilities for vocal social  
131 learning have recently been demonstrated in monkeys (Lemasson et al, 2005; Takahashi et  
132 al., 2015). The architecture and connectivity of avian and mammalian brains are much  
133 more similar than had been recognized previously (Reiner et al., 2004). For instance, avian  
134 pallial 'song' regions bear functional similarities with human auditory and motor cortices  
135 and the importance of the basal ganglia for both speech and birdsong is starting to be  
136 understood mechanistically (Doupe et al., 2005; Jarvis et al., 2005; Mooney, 2009). These  
137 aspects and others consolidate birdsong as the biological model of choice to study the  
138 behavioral, molecular and cellular substrates of vocal learning, an important component of  
139 language acquisition (Bolhuis et al., 2010). Studies that cannot be conducted on humans

140 for obvious ethical reasons can easily be done with captive populations of oscine songbirds,  
141 and exposing a bird to its own song is a useful method to investigate the neural substrates  
142 for individual recognition. Here, we are not reviewing the literature dealing with exposure  
143 to self-produced vocalizations in mammals, but it is likely that the number of studies would  
144 be greatly outnumbered by those conducted in birds.

145 Besides the aspects linked to vocal learning, recent studies have shown that birds and  
146 mammals faced a similar selection pressure for complex cognitive abilities, resulting in the  
147 evolution of a comparable neural architecture of forebrain association areas as well as in  
148 cognitive operations (Butler et al., 2005). The dorsal ventricular ridge (DVR) of the avian  
149 brain contains neuronal populations homologous to those present in different layers of the  
150 mammalian neocortex. The neurons of the avian DVR and mammalian cortex are nearly  
151 identical in both their morphology and constituent physiological properties. Structural  
152 homologies were also identified using molecular and immunohistological techniques. In  
153 particular, neurotransmitters, neuropeptides, and receptors specific to particular neuronal  
154 populations within mammalian brain regions have been localized to homologous avian  
155 brain regions (Edelman & Seth, 2009, Figure 1).

156 This high degree of evolutionary convergence is especially apparent in the cognitive  
157 abilities of corvids and parrots, big-brained birds whose forebrains have a relative size the  
158 same as those of apes, and who behaviorally perform at a comparable level with apes in  
159 many domains such as episodic memory, tool-use and theory of mind (Figure 2; Emery &  
160 Clayton, 2004; Emery, 2006; Güntürkün & Bugnyar, 2016; Van Horik & Emery, 2011). In  
161 the field of animal cognition, variants of the mirror test have been used in birds but so far

162 only magpies have been shown to recognize their own reflection (Prior et al., 2008). We  
163 will discuss this result later.

164 In the case of mirror self-recognition, the issue of self-perception is addressed directly. As  
165 we presented before, the perception of self is an important issue in the social life of a bird  
166 during encounters with other individuals such as during mate choice.

167 The aim of this article is to give a state of the art review of the different studies dealing  
168 either directly or indirectly with the perception of self in birds across disciplines such as  
169 developmental and cognitive neuroscience, animal psychology, ethology and behavioral  
170 ecology. Birds have been exposed to self-stimuli through different sensory modalities:  
171 vision, olfaction and audition.

172 For a long time, it was believed that birds had a poor sense of smell. But as we will  
173 summarize, recent studies have shown that olfactory signals play an important role in  
174 orientation and the social life of several bird species (Caro et al., 2015).

175 Finally, playback of birds' own vocalizations have been extensively used both in the field  
176 and in the laboratory and in many species of birds. Oscine songbirds exhibit an especially  
177 strong response to the broadcast of their own song, both at the behavioral and at the neural  
178 levels. Such experiments have helped us decipher the mechanisms of vocal  
179 coding/decoding for example during socio-sexual interactions such as territory defense.

180 Exposing a bird to its own vocal signature is a useful means to investigate the neural  
181 substrates of individual recognition; a fruitful topic of research that has been barely  
182 addressed in other sensory modalities. This topic has been also barely addressed in  
183 mammals.

184 Vocal learning allows fine vocal adjustments in some bird species and the perception of  
185 self can also be addressed by an analysis of vocal labeling, namely the use of calls to  
186 address a specific individual. Such vocal labeling has been shown in some parrot species  
187 and people rearing parrots and corvids usually give names to their pets/experimental  
188 subjects.

189 In this review, we want to stress the importance of experience and the social environment  
190 during development in self-recognition; these aspects can easily be monitored in captive  
191 populations of birds. In the concluding part of this review, we will propose future directions  
192 to study the perception of self in birds including the multimodality of the perception of self  
193 (use of different sensory modalities) and other aspects linked to emotions that could echo  
194 recent realization in animal welfare.

195

## 196 **2. Visual representations**

197

### 198 ***2.1. Self-referent visual phenotype matching***

199

200 Most birds learn conspecific characteristics from their parents and siblings. They probably  
201 also take into account their own phenotype, and later match features of encountered  
202 individuals to that template through self-referent phenotype matching. Such self-  
203 referencing was studied with cross-fostered and naïve (raised in social isolation) chicks  
204 (*Gallus domesticus*, Salzen & Cornell, 1968; Vidal, 1975). Salzen and Cornell (1968)  
205 conducted a series of experiments to test the hypothesis that self-perception explains  
206 preferential choices of conspecifics by birds raised in isolation. They painted chicks with

207 different colors and kept them in social isolation for 8 days before testing them in a 2-  
208 choice experiment with a companion from the same color and another one with a different  
209 color. The authors conclude that the self-perception hypothesis is tenable at least if  
210 perception through reflection in water is included. Indeed, chicks reared in isolation with  
211 no drinking trough (water was administered by pipette directly in the crop) failed to show  
212 any tendency to choose a companion with their own color (Salzen & Cornell, 1968). Even  
213 with modifications to prevent self-reflection in water such as painting the bottom of  
214 drinking trough in white (Vidal, 1975), there is evidence that birds can perceive their  
215 shadow. For example, domestic roosters exhibit courtship displays towards their shadow  
216 (Vidal, 1975). Vidal (1975) observed that an isolated cock perceived and fixated on parts  
217 of its own body (self-fixation), but remained able to orient and adjust its behavior towards  
218 a partner resembling itself. Social isolation cannot prevent proprioceptive feedback that  
219 can complete the visual information that an animal cannot assess without a mirror (Vidal,  
220 1975). It has been acknowledged for a long time that experimentally isolated animals are  
221 indeed never isolated from themselves (Lehrman, 1953).

222 In interspecific brood parasites, however, early social learning could lead to species  
223 recognition errors because young are reared among heterospecifics. In an experiment,  
224 feather color of hand-reared fledglings of the parasitic brown-headed cowbird (*Molothrus*  
225 *ater*) was manipulated. Juvenile cowbirds approached more quickly and associated  
226 preferentially with individuals that were colored similarly to themselves (Hauber et al.,  
227 2000). This result eliminates the possibility that their recognition template was genetically  
228 determined.

229

230 **2.2. Exposure of a bird to its own reflection in a mirror**

231

232 Mirror-induced self-directed behavior has been studied in several species of birds. Most of  
233 the species tested so far failed to show self-directed behavior in front of their mirror-image.  
234 They have been tested either in the wild (chickadees *Parus atricapillus*, Censky & Ficken,  
235 1982; glaucous-winged gulls *Larus glaucescens*, Stout et al., 1969) or in the laboratory in  
236 captivity (Blue grouse *Dendragapus obscurus*, Stirling, 1968; budgerigars *Melopsittacus*  
237 *undulatus* and house sparrows *Passer domesticus*, Gallup & Capper, 1970; a kea *Nestor*  
238 *notabilis*, Diamond & Bond, 1989; zebra finches *Taeniopygia guttata*, Ryan 1978; cedar  
239 waxwings *Bombycilla cedrorum* and Juncos *Junco hyemalis*, Andrews, 1966; Lovebirds  
240 *Agapornis roseicollis*, Delsaut & Roy, 1980; African Grey Parrot *Psittacus erithacus*:  
241 Pepperberg et al., 1995; Jungle Crow *Corvus macrorhynchos*: Kusuyama et al., 2000; Java  
242 Sparrow *Padda oryzivora*: Watanabe, 2002; New Caledonian Crow *Corvus moneduloides*:  
243 Medina et al., 2011; Jackdaw *Corvus monedula*: Soler et al., 2014). Many of them respond  
244 to their self-image with social behaviour, i.e. treating the mirror-image as if it were a  
245 conspecific. Some bird species exhibit aggressive behavior in the presence of a mirror  
246 while others exhibit courtship displays. A Flamingo (*Phoeniconais minor*) flock exhibited  
247 marching displays in front of mirrors (Pickering & Duverge, 1992). Some bird species such  
248 as house sparrows, parakeets and zebra finches exhibit a preference for mirror image  
249 stimulation over visual access to a conspecific (Gallup & Capper, 1970; Ryan, 1978). This  
250 preference was shown in the absence of auditory cues. The authors hypothesized that the  
251 mirror image could be perceived as a supernormal stimulus since the mirror image would  
252 always be both predictable and compatible with the animal's behavior. Mirrors are often

253 used as a social substitute to reduce stress in highly social birds, such as starlings (*Sturnus*  
254 *vulgaris*, Henry et al., 2008) and zebra finches, kept in social isolation for laboratory  
255 experiments. Female pigeons (*Columba livia*) would ovulate when exposed to her own  
256 reflection in a mirror (Matthews, 1939). It is noteworthy that the length of exposure and  
257 size of the mirror vary greatly across these studies. So far, MSR capacity using an adapted  
258 version of the experimental procedure developed by Gallup (1970) has been found only in  
259 one bird species, the magpie (Prior et al., 2008; Figure 3). The authors used a sticker as a  
260 mark that was stuck under the beak, in the throat area, outside the magpies' visual field.  
261 Two magpies out of five were capable of removing the sticker by scratching with their foot  
262 in mirror-present sessions. The results obtained in magpies have important biological and  
263 cognitive implications because the fact that magpies were able to pass the mark test means  
264 that mirror self-recognition evolved independently in the magpie and great apes (which  
265 diverged 300 million years ago) and that the neocortex (which is not present in the bird's  
266 brains as mentioned before) is not a prerequisite for MSR as previously believed (Prior et  
267 al., 2008). Using the same experimental procedure, Soler and colleagues (2014) failed to  
268 show MSR in jackdaws: they showed mark-directed behavior in the mirror but also in the  
269 no-mirror condition. Moreover, the authors pointed out potential methodological problems  
270 with the study on magpies. According to them, magpies might have detected the sticker  
271 using tactile sense through feather sensitivity. They suggest to use more appropriate  
272 marking methods for future avian marking tests such as using paint that does not  
273 agglomerate the feathers or, at least allows for the perfect separation of feathers when dried,  
274 for instance typing correction fluid. However, as two of the magpies showed significantly  
275 more mark-directed behavior when tested in front of a mirror than in the absence of a

276 mirror, tactile sense cannot be the sole explanation for their mark-directed behavior.  
277 Another interesting result from the magpie and the jackdaw studies is that in both  
278 experiments the birds showed self-contingent behavior (i.e., they moved their head or the  
279 whole body back and forth in front of the mirror in a systematic way). In the magpie study,  
280 the 3 birds that showed self-contingency behavior also showed mark-directed enhanced  
281 behavior in the mark test (this was significant for two of them).

282 Mirror studies were also conducted in two other corvid species, namely the jungle crow  
283 (Kusayama et al., 2011) and the New Caledonian crow (Medina et al., 2011). New  
284 Caledonian crows, but not jungle crows, had the possibility to explore behind the mirror as  
285 in the magpie study. No self-contingency behavior was reported for the jungle crows; the  
286 birds may not have received enough mirror experience though, since they had only 3  
287 sessions of 25 minutes with a vertical mirror, and the same amount of time with a horizontal  
288 mirror. Exposure to mirrors was also very limited in the study on New Caledonian crows,  
289 only 3 sessions of 10 minutes. The authors reported that they did not observe self-  
290 contingent behavior, but that 3 juvenile crows (out of 10 birds) reacted to their mirror image  
291 by repeatedly performing “peekaboo” behavior. Such behaviors could in fact be a kind of  
292 self-contingent behavior, and were also observed in one of the two young grey parrots  
293 tested by Pepperberg et al. (1995). The other grey parrot also showed a kind of self-  
294 contingent behavior: in 3 sessions out of 15, she put a foot against the mirror and placed  
295 her head as to provide a simultaneous view of her foot and its mirror image. African grey  
296 parrots (Pepperberg et al., 1995) and New Caledonian crows (Medina et al., 2011) also  
297 showed the ability to use a mirror to locate hidden food.

298 In many studies, the mirror was presented in a vertical position. The horizontal mirror  
299 image may mimic a reflection from a water surface and it would be more natural for the  
300 bird to see the image as its own. On the other hand, vertical images are more natural than  
301 the horizontal ones if they are seen as images of conspecifics. Indeed, an upright mirror  
302 was more effective for evoking social aggressive behavior than a horizontally placed mirror  
303 (Kusayama et al., 2000; Pepperberg et al., 1995).

304 To sum up, self-contingent behavior was observed (at least in some individuals) in 3 out  
305 of 4 studies in corvids and in the one study with parrots. Only two mark tests have been  
306 conducted in birds: the magpie study, in which some of the birds passed the test, and the  
307 jackdaw study, which was not conclusive, since the birds showed mark-directed behavior  
308 in both the mirror and no-mirror conditions, probably because they sensed the sticker on  
309 their feathers. Therefore, although more experiments are needed (particularly conducting  
310 mark tests with a design ensuring that tactile cueing is not possible) these data are very  
311 promising and hint to some ability for MSR in corvids and parrots. These abilities would  
312 be consistent with high performance in these birds in tasks related to theory of mind  
313 (Bugnyar et al., 2016; Dally et al., 2006; Emery & Clayton, 2001; Péron et al., 2010; 2011).

314 It is extremely crucial to check whether self-directed behavior in birds represents a  
315 spontaneous response to seeing their own body in the mirror. Pigeons were successfully  
316 trained to peck at a spot on their bodies that could only be seen with the aid of a mirror  
317 (Epstein et al., 1981). Thompson & Contie (1994) failed to replicate these results although  
318 the exact details of the training procedure had not been documented and training could  
319 have been a crucial factor in obtaining positive results. Indeed, Uchino and Watanabe  
320 (2014) recently revisited self-recognition in pigeons using a similar procedure as Epstein

321 and collaborators. They observed that after extensive training with food reinforcement, two  
322 pigeons spontaneously integrated the learned self-directed and mirror-use behavior and  
323 displayed self-directed behavior in a mark test. In a previous experiment, the authors  
324 trained pigeons to respond to live video images of themselves and not to respond when  
325 they viewed prerecorded videos (Toda & Watanabe, 2008). Pigeons' discrimination of self-  
326 movies was based on the temporal contiguity between their behavior and visual feedback  
327 since their relative response rate to delayed presentation of live self-movies gradually  
328 decreased as the temporal discrepancy between their own behavior and the corresponding  
329 video increased (Toda & Watanabe, 2008). These results suggest that the visual properties  
330 of self-image are not the primary cue for self-recognition, and the visual-proprioceptive  
331 contingency between a subject's action and the corresponding visual scene reflected in a  
332 mirror might be an essential component. If so, subjects might not require complex cognitive  
333 and social abilities to discriminate self from others (Toda & Watanabe, 2008). That said,  
334 pigeons need extensive training for this form of self-recognition which contrasts drastically  
335 with humans and other species that do not need such training. This is the case with the  
336 magpies that exhibited self-related behavior in front of a mirror after a rather short  
337 cumulative exposure time and without being specifically trained to do so (Prior et al.,  
338 2008).

339

### 340 **3. Exposure of a bird to its own smell**

341

342 In several petrel species of burrow nesters, the burrow olfactory signature is important for  
343 homing. Using a T-maze experiment, de Léon et al. (2003) showed that European storm

344 petrel chicks (*Hydrobates pelagicus*) are able to recognize their own odor and that this odor  
345 leads them back to the nest.

346 Using a similar kind of maze experiment, it was shown that Antarctic prions (*Pachyptila*  
347 *desolata*) preferred their own odor when presented against an odorless blank cotton, thus  
348 demonstrating the bird's capacity to perceive self-odor (Bonadonna & Nevitt, 2004).  
349 Further work on this species and blue petrels (*Halobaena caerulea*) demonstrated that these  
350 birds could discriminate between their own and their mates' odors. They are attracted by  
351 their mate's odor, and they prefer the odor of a conspecific bird to their own (Bonadonna  
352 & Nevitt, 2004; Mardon & Bonadonna, 2009). Such behavior could be related to kin  
353 recognition and inbreeding avoidance (Bonadonna, 2009). Another study has shown that  
354 Humboldt penguins (*Spheniscus humboldti*) preferred unfamiliar non-kin odors over  
355 unfamiliar kin odors (Coffin et al., 2011). This study provided evidence of odor-based kin  
356 discrimination in a bird, probably through a mechanism of phenotype matching. Olfactory  
357 preferences may vary with age and/or social context so that self-odor avoidance may be  
358 developed only at sexual maturity.

359 Although olfaction was often believed to be unimportant in songbirds, zebra finch and  
360 Bengalese finch (*Lonchura striata*) females (but not males) prefer the odor of their own  
361 nest over a foreign conspecific nest (Krause & Caspers, 2012). Young zebra finches also  
362 prefer the odor of their natal nest over a foreign nest odor (Caspers & Krause, 2010). This  
363 preference is learned very early, in the 48h after hatching, or maybe even before hatching,  
364 as shown by cross fostering experiments (Caspers et al., 2013, Krause et al., 2012).

365 As discussed above, some birds can recognize their own odor, but this could be based on a  
366 simple familiarity rather than on a concept of self. To separate between these alternatives

367 is not easy. Some matching-to-sample experiments could be conducted in which a bird  
368 would have to match the odor of different conspecifics, including itself, to vocalizations or  
369 images. However, to solve this task, the bird would have to identify his own odor but also  
370 his own vocalizations or image. Some priming experiments ( exposure to one stimulus to  
371 influence the response to another stimulus) using different modalities could also be  
372 informative in this respect.

373

#### 374 **4. Exposure of a bird to its own vocalizations**

375

376 As mentioned before, birds are of particular interest regarding vocalizations since many  
377 species (mostly oscine songbirds representing about half of all bird species) exhibit vocal  
378 production learning, which is the capacity to imitate sounds from the environment, mainly  
379 those from the social environment produced by conspecifics. In other, non-vocal learning  
380 species, such as columbiforms (e.g. pigeons, doves) and galliforms (e.g. chickens, quails),  
381 the structure of vocalizations is under a strong genetic determinism despite some  
382 rudimentary vocal plasticity reminiscent to that described recently in non-human primates  
383 (Derégnaucourt et al., 2009). Some vocal learners, like starlings and canaries, are able to  
384 learn new songs throughout their lives, sometimes during limited periods of time during  
385 the year, while others, like zebra finches, can only learn to imitate a song model during a  
386 sensitive period in the first year of life (Brainard & Doupe, 2002). Some species, such as  
387 the zebra finch, produce a single (short duration) song while others, such as the nightingale  
388 (*Luscinia megarhynchos*), possess a song repertoire composed of hundreds of different  
389 song types (Catchpole & Slater, 2008).

390 **4.1. Experiments in the wild**

391

392 To our knowledge, all experiments in the wild concern oscine songbirds. The first  
393 experiments using the Bird's Own Song (BOS) aimed at understanding the function of  
394 different songs in the bird's repertoire (Great Tit *Parus major*: Krebs et al., 1981; Brémond,  
395 1968). Some studies investigated more subtle aspects such as song timing during vocal  
396 exchanges in nightingales (Hultsch & Todt, 1982), European blackbirds (*Turdus merula*;  
397 Todt, 1970, 1975, 1981; Wolffgramm & Todt, 1982) and great tits (Weary et al., 1990). In  
398 most of the cases, the broadcast of the BOS has been used as a control in experiments of  
399 simulated territorial intrusion with the idea that the birds could use their BOS as a reference  
400 against which other songs could be evaluated (Mc Arthur, 1986). In such experiments,  
401 birds exhibit different behavioral responses that could be measured such as their latency to  
402 react, their approach to the loudspeaker, the number of songs produced and the acoustic  
403 similarity between the songs produced and the song broadcast ('song matching').

404 In some species, behavioral responses to song playbacks are maximal when the song  
405 broadcast is the BOS. For example, in great tits (Falls et al., 1982), western meadowlarks  
406 (*Sturnella neglecta*; Falls, 1985) and song sparrows (Stoddard et al., 1992), song matching  
407 was maximal following broadcast of the BOS in comparison with neighbor and stranger  
408 songs. In other studies, the BOS produced an intermediate response strength falling  
409 between that elicited by the songs neighbors and strangers (ovenbirds *Seirus aurocapillus*:  
410 Weeden & Falls, 1959; white-throated sparrow *Zonotrichia alhicollis*: Brooks & Falls,  
411 1975; swamp sparrows *Melospiza georgiana*: Searcy et al., 1981; red-winged blackbirds  
412 *Agelaius phoeniceus*: Yasukawa et al. 1982).The majority of birdsong research concerns

413 male song, but females from many oscine songbird species also sing (Odom et al., 2014).  
414 In the red-winged blackbird, females gave statistically similar responses to playback of  
415 BOS and stranger songs (Beletsky, 1983).  
416 In song sparrows, results differ between different studies and this highlights the necessity  
417 to take into account the methodological aspects of the playback procedure, the response  
418 measures and the statistical treatment of the data. Some studies have shown that the  
419 response of male song sparrows to the BOS is not different than the response to a stranger  
420 song, both in terms of aggression (approach to the speaker; Searcy et al., 1981) and song  
421 matching (Stoddard et al., 1992). In contrast, in the only study conducted with the goal to  
422 demonstrate auditory self-awareness in birds, Mc Arthur (1986) observed that the territorial  
423 response was minimal during the broadcast of the BOS and that the strength of the  
424 territorial response was inversely correlated with the similarity of the stimulus song to the  
425 BOS. Nevertheless, song matching was also higher for the BOS than for a stranger song  
426 acoustically dissimilar to the BOS. Some of these results were not statistically significant.  
427 It is also worth mentioning that these studies were done before the advent of the  
428 multivariate-measure approach (such as principal component analysis) that became a  
429 standard in the design of playback experiments since the 90's (Mc Gregor, 1992).  
430 How can we interpret these results? In the case when the bird exhibits a strong response, it  
431 may be that he perceived the BOS as a fully shared stranger song. One's own sounds might  
432 be perceived as different since the normal bone conduction that is present when emitting a  
433 sound is absent from the playback sound. In the same way the human voice sounds strange  
434 when heard from a tape, a bird could react to his BOS as though it were produced by a  
435 stranger. Response to BOS in song sparrows is similar to response to stranger song both in

436 terms of matching (Stoddard et al. 1992) and aggression (Searcy et al. 1981 but see Mc  
437 Arthur, 1986), and another study suggest that there is no voice recognition in this species  
438 (Beecher et al., 1994). However, a bird could also recognize his BOS and react strongly  
439 because he is surprised to hear himself. He would approach the loudspeaker or even sing  
440 in order to investigate what is happening; therefore, very detailed description of the bird's  
441 behaviors would be needed to discriminate between a purely territorial response and a  
442 surprised response.

443 When the response to the playback of the BOS is weak, auditory self-awareness could be  
444 suggested but there are also other alternative hypotheses (Mc Arthur, 1986). Habituation  
445 and familiarity could be involved. One would expect a male to hear his own song more  
446 often than that of any of his neighbors. If a male's perception of his own song as he sings  
447 it is the same as his perception of its BOS playback (one can only speculate about the  
448 degree to which a bird's skull distorts the perception of its song as it is sung), a weaker  
449 response to BOS than to neighbor song would be predicted. For reasons already mentioned  
450 above, the results obtained by Mc Arthur (1986) and his interpretation of the data have  
451 been questioned (Suarez & Gallup, 1987; Mc Arthur 1987), and most results obtained in  
452 song sparrows show that birds consider BOS as stranger songs.

453 Brooks and Falls (1975) provide an explanation for an intermediate response to the  
454 playback of BOS (responses measuring between those to stranger and to neighbor songs).  
455 During the broadcast of a song in the territory of a focal bird, song activity from his  
456 neighbors is sometimes observed and this vocal activity could affect the behavioral  
457 response of the focal bird. During the broadcast of a stranger song, the strong response of  
458 a focal bird could be enhanced by the strong response of his neighbors. During the

459 broadcast of his BOS, his neighbors should recognize him and act accordingly by singing  
460 less. This low activity might affect the response of the focal bird. But the BOS may also  
461 sound intermediate in terms in familiarity: less familiar than a neighbor song because of  
462 the bone distortion, but more familiar than a completely stranger song.

463 The different reactions to the BOS playback are also probably linked to the different socio-  
464 ecological aspects of the different species that were tested. During song playback, males  
465 of some species engage in counter-singing: they produce the song that best resembles the  
466 playback song (Bremond, 1968; Falls et al., 1988). Indeed, many species of oscine  
467 songbirds often engage in copying and matching sounds through which they address each  
468 other. Depending on the context, they could use either song type matching, (producing the  
469 same song they hear) or repertoire matching (producing a shared song type while avoiding  
470 singing the same song type). Playback of the BOS have been used extensively in several  
471 experiments on matching in song sparrows (Akçay et al., 2011, 2013, 2014; Anderson et  
472 al. 2005; Searcy et al., 2013; Stoddard et al., 1992). For example, song sparrows use song  
473 type matching when defending their territory against an unknown male, but avoid it when  
474 interacting with known neighbors with whom they use more subtle repertoire matching  
475 (Beecher & Campbell, 2005). Repertoire matching may allow addressing a neighbor in a  
476 more affiliative or neutral way. For example, song sparrows, western meadowlarks and  
477 great tits do not type-match a neighbor's song but do the BOS or a stranger's song (Falls,  
478 1985; Falls et al., 1982; Stoddard et al., 1992). In some species such as the great tit, if the  
479 theme broadcast is absent from the bird's repertoire, it will reply with the theme closest in  
480 structure within its own repertoire (Krebs et al., 1981). This form of categorization suggests  
481 that there is an auditory reference to which the stimulus is compared before production

482 occurs. Such a reference is the result of different influences, particularly learning. More  
483 recently, playback of the BOS brought to light a turnover in repertoire composition over a  
484 relatively short period in great tits (Franco & Slabbekoorn, 2009).

485 Another hypothesis was that the BOS could be used as a reference in localizing the emitter:  
486 degradation of a song over distance may be used as a cue if the male has his own,  
487 undegraded rendition of the song to use as a standard (Morton, 1982). Mc Gregor & Krebs  
488 (1984) have shown that great tits respond less strongly to degraded than to undegraded  
489 song? not only if they are sung by the birds themselves (BOS) but also if they are produced  
490 by neighbors. This result suggests that birds do not necessarily need to have a song in their  
491 own repertoire to use sound degradation as a distance cue but rather to be familiar with the  
492 song broadcast. This finding that birds can assess the degree of degradation of songs that  
493 they do not sing, supports the idea that birds learn more songs than they sing.

494 Altogether, these experiments have shown that familiarity and acoustic similarity with the  
495 BOS are taken into account by the focal bird to provide an appropriate behavioral response  
496 (song matching, approach to the loudspeaker) during song broadcast.

497

#### 498 ***4.2. Experiments in the laboratory***

499

500 The hypothesis that the BOS is used as a reference against which other males' songs are  
501 evaluated was first proposed by Hinde (1958) based on his experiments with hand-reared,  
502 tutored chaffinches (*Fringilla coelebs*). He tutored young males with abnormal songs,  
503 which they learned and later sang as adults. When the adults heard normal chaffinch songs  
504 and their abnormal BOS, they produced more songs in response to the abnormal BOS.

505 Similarly, adult zebra finches (*Taeniopygia guttata*) express a robust behavioral preference  
506 for the playback of their BOS compared with conspecific male song in a phonotaxis  
507 experiment (Ramage-Healey et al., 2010). However, the tutor song is a stronger stimulus  
508 than the BOS: finches exposed either passively or through operant conditioning to the tutor  
509 song during development preferred the training song over a novel song as well as over their  
510 BOS as adults (Adret, 1993). Using operant conditioning, it was shown that males trained  
511 to discriminate between their own song and another song from their aviary reached  
512 criterion in a fewer number of trials than males that had to discriminate between songs  
513 from their own aviary, with the most training required by males discriminating between  
514 songs they had not heard before (Cynx & Nottebohm, 1992). While most studies  
515 investigated songs in oscine songbirds, it is worth mentioning that the ‘autogenous  
516 reference’ could be also used in non-vocal learner species through self-referent phenotype  
517 matching. For example, in a two-choice experiment, neonate chicks (*Gallus domesticus*)  
518 exhibited a preference for a speaker broadcasting a maternal call with acoustic features  
519 resembling those of the bird’s own twitter rather than a speaker broadcasting a maternal  
520 call with acoustics dissimilar to their own twitter (Guyomarc’h, 1973). Similarly, chicks  
521 raised in mixed flocks of two varieties, when tested in a Y-maze, learn to go to chicks of  
522 their own variety more readily than to those of the other variety (Howells & Vine, 1940).  
523 Besides genetic influences, it is also plausible that the chick’s experience with its own  
524 chirping could be used as a source of differential learning (Schneirla, 1946).  
525 At the neural level, the earliest attempts to record singing-related activity in the brain of  
526 freely behaving oscine songbirds (canaries and white-crowned sparrows) detected  
527 increased activity not only during singing but also when the BOS was broadcast through a

528 speaker (Mc Casland & Konishi, 1981). This paradigm, used in more than one hundred  
529 studies so far, could permit to look for the neural template that determines the BOS.  
530 Songbirds have specialized, discrete brain regions for song production and learning (Figure  
531 4). The Song Motor Pathway (SMP) is involved in song production and certain aspects of  
532 song learning, and the Anterior Forebrain Pathway (AFP) that connects with the motor  
533 pathway, is essential for sensorimotor learning and adult song plasticity. These two  
534 pathways together are usually called the ‘song control system’ (Brainard & Doupe, 2002).  
535 The sensorimotor nucleus HVC (used as a proper name) which belongs to the SMP was  
536 the first song nucleus in which song-selective neurons were observed (Mc Casland &  
537 Konishi, 1981). Most neurons from the HVC that are responsive to song playback are  
538 highly selective for the BOS, firing more to forward auditory playback of the BOS than to  
539 reverse BOS or conspecific songs (Margoliash, 1983, 1986; Margoliash & Konishi, 1985;  
540 Mooney, 2000).

541 In contrast, field L neurons from the primary auditory regions, which are presumed to be a  
542 source of auditory input to HVC, do not exhibit selectivity for BOS (Margoliash, 1986;  
543 Boumans et al., 2008). These observations implicate song (motor) learning in shaping the  
544 response properties of HVC but not of auditory neurons.

545 It has been proposed that HVC auditory neurons may contribute to a bird’s ability to  
546 discriminate among conspecific songs by acting as an ‘autogenous reference’ during the  
547 perception of those songs (Margoliash, 1986). During the process of song acquisition,  
548 auditory neurons in the song control system are shaped to respond best to the BOS  
549 (Margoliash, 1983; Doupe & Konishi, 1991).

550 This pattern of self-responsiveness is even found in adult birds raised without a tutor  
551 indicating that self-experience is a critical factor in shaping BOS-selectivity (Kojima &  
552 Doupe, 2007). Furthermore, BOS-selective auditory responses in HVC and the AFP  
553 emerge as sensorimotor learning progresses (Volman, 1993; Doupe, 1997; Solis & Doupe,  
554 1999; Nick & Konishi, 2005a,b).

555 Using lesions both at the central and peripheral levels, the development of the selectivity  
556 for the BOS and its neural template could be investigated (Ramage-Healey et al., 2010;  
557 Roy & Mooney, 2007).

558 Male finches muted during the sensitive period for song learning responded to playbacks  
559 at chance levels as adults, showing no preferences for individual conspecific songs. These  
560 results suggest that the acquisition of the BOS may contribute to the perceptual processing,  
561 recognition, or discrimination of different conspecific songs (Pytte & Suthers, 1999). This  
562 experiment and others support a hypothesis which is an avian parallel to the motor theory  
563 of speech perception in humans (Williams & Nottebohm, 1985). This theory proposes that  
564 speech is perceived not just as a sound but as a series of articulatory gestures (Liberman &  
565 Mattingly, 1985).

566 Many techniques have been applied to investigate the functional organization of the song  
567 system. Although single-cell electrophysiology has been the most successful, other  
568 techniques such as gene expression and brain imaging have helped to decipher the neural  
569 coding of the BOS (Kimpö & Doupe, 1997; Boumans et al., 2008; Van der Kant et al.,  
570 2013).

571 Taken together, these results suggest that BOS-selective neurons in oscine songbirds could  
572 provide an 'error signal' that promotes changes in song production when a mismatch is

573 detected between auditory feedback from self-song and the memorized song template, and  
574 could thus have a role in both song learning and maintenance (but see Leonardo, 2004). A  
575 second function might be the perception of conspecific song. These functions are not  
576 necessarily mutually incompatible. They could also be at play in non-songbird species. For  
577 example, the influence of auditory feedback on sexual development has also been  
578 extensively studied in a non-vocal learner species, the ring dove (*Streptopelia risoria*). In  
579 this species, courtship is initiated by males. Males' coos (the equivalent of song in oscine  
580 songbirds) is an integral feature of the courtship. When the female is motivated, she  
581 produces her own 'nest coos' in response to the male's coos. Several experiments in intact,  
582 muted, and deafened female doves have shown that a female's own nest coos affect her  
583 endocrine state (Cheng & Durand, 2004). For example, playback of the female's own coos  
584 was the most effective stimulus for her follicular development, but playback of other  
585 female coos was also more effective than playback of male song.

586 Most studies of the song selectivity of HVC neurons have been performed in the zebra  
587 finch, a species that sing a single song (Catchpole & Slater, 2008). Studies in other songbird  
588 species that sing several song types or longer song have expanded this picture and provided  
589 new insights into the neural coding of song in the HVC (Nakamura & Okanoya, 2004;  
590 George et al., 2005; Nealen & Schmidt, 2006; Allende et al., 2013). For example, the  
591 swamp sparrow is a species that sings 2–5 simple song types, each consisting of the  
592 repetition of a single syllable. Some neurons in HVC exhibit both motor-related activity  
593 and auditory responses to a playback of a BOS. As such, these neurons are reminiscent of  
594 the mirror neurons discovered in the monkey brain (Prather et al., 2008).

595 Selectivity of HVC neurons is modulated by the behavioral state of the animal, and  
596 interspecific differences have been observed (Margoliash & Schmidt, 2010). For example,  
597 in the zebra finch, neurons with responses to BOS playback in anaesthetized or sleeping  
598 animals do not always show these responses when finches are awake, indicating that  
599 auditory responses to sounds are ‘gated’ by the behavioral state of the bird and little or no  
600 auditory-evoked activity is detectable in the HVC or the AFP during periods of  
601 wakefulness (Cardin & Schmidt, 2003). In contrast, song-evoked auditory responses have  
602 been detected in song system of awake sparrows, starlings, canaries and Bengalese finches,  
603 indicating that the ‘gate’ between the auditory and song systems remains open in these  
604 species (McCasland & Konishi, 1981; George et al., 2005; Margoliash, 1986; Nealen &  
605 Schmidt, 2006; Prather et al., 2008; Fujimoto et al., 2011).

606 In the zebra finch, timing and structure of neural activity elicited by the playback of the  
607 BOS during sleep matches activity during daytime singing in many brain nuclei of the song  
608 control system such as the HVC and the RA (Dave & Margoliash, 2000; Hahnloser et al.,  
609 2002). Additionally, ‘spontaneous’ activity of these neurons during sleep matches their  
610 sensorimotor activity, a form of song ‘replay.’ These data suggest a model whereby  
611 sensorimotor correspondences are stored during singing but do not modify behavior, and  
612 off-line comparison (e.g., during sleep) of rehearsed motor output and predicted sensory  
613 feedback is used to adaptively shape motor output (Derégnaucourt et al., 2005; Margoliash  
614 & Schmidt, 2010). To conclude, the perception of the BOS and to some extent of the self  
615 is affected by the behavioral state and can also be addressed in sleeping birds.

616

617

618 **5. Use of learned signals as individually specific labels**

619

620 It is well known, in both vocal and non-vocal learners that animals can recognize a  
621 conspecific based on acoustic cues. Addressing of specific individuals in a communication  
622 network can be achieved by vocal labeling, where a specific vocalization is linked to a  
623 specific individual (Balsby et al., 2012). In captivity, animals can be easily trained to  
624 associate a sound, often a human spoken word, with a personal reward such as food or care.  
625 For example, using a combination of classical and operant conditioning procedures, pigs  
626 living in a group can be trained to enter a feeder only after an individual acoustic signal  
627 has been presented. This call feeding procedure minimizes queuing and thereby reduces  
628 aggression, stress and injuries associated with feeding (Manteuffel et al., 2011). In the wild,  
629 there is evidence that bottlenose dolphins recognize their own vocal signature (King &  
630 Janik, 2013). In birds, some species of parrots have been found capable of using arbitrary,  
631 learned signals to label or name objects in experimental studies (Pepperberg, 1981). In  
632 captivity, parrots can learn to pronounce their own name and to respond to it more than to  
633 the name of other individuals (Bovet, Giret & Péron, unpublished obs.), but, as in the case  
634 of pigs cited above, this could be the result of a simple conditioning effect that is not  
635 necessarily linked to self-awareness. Researchers working with ravens (*Corvus corax*) can  
636 also easily get the bird's attention by calling its name (Bugnyar et al., 2016). One raven  
637 raised in captivity in isolation who was named Goliath would produce its name when his  
638 caretaker would enter in the room (Gwinner, 1964). There is also evidence that a kind of  
639 naming is also present in the natural communication system of some bird species. For  
640 example, spectacled parrotlets (*Forpus conspicillatus*) use contact calls to refer to a social

641 companion and thus label or ‘name’ their conspecifics (Wanker et al., 2005; Figure 5).  
642 Such labelling could help capturing the attention of and further interaction with a particular  
643 individual in the social group, similarly to humans calling out the name of an associate at  
644 a noisy social gathering. It is possible that these contact calls used as labels or ‘names’  
645 could be imitations of the addressee’s calls but that hypothesis has not been tested yet in  
646 this species (Bradbury & Balsby, 2016). Such imitation have been observed in orange-  
647 fronted conures (*Aratinga canicularis*). Conures can imitate contact calls almost  
648 immediately upon hearing them (Balsby & Bradbury, 2009). In this fusion/fission species  
649 that is non-territorial and that lives in small groups, vocal matching is observed in the wild  
650 prior to flock fusion and might represent some form of negotiation (Balsby & Bradbury,  
651 2009). Orange-fronted conures can use imitation of contact calls to address specific  
652 individuals of a flock (Balsby et al., 2012). The authors argue that the fission-fusion flock  
653 dynamics of many parrot species has been an important factor in evolving conures’ and  
654 other parrots’ exceptional ability to imitate (Bradbury & Balsby, 2012).

655

## 656 **6. Conclusion and future directions**

657

658 Exposing an animal to its own image, smell or vocalizations experimentally has helped us  
659 understand how individuals process social information. Since the perception of self can be  
660 achieved using different sensory modalities, it would be of interest to investigate whether  
661 each modality controls a different level of self or if these different levels are linked to each  
662 other in order for an individual to build an integrative and unified template of self. In many  
663 species, subjects are able to match the voice of a familiar conspecific to its image. For

664 example, large-billed crows are sensitive to identity congruence between the visual  
665 presentation of a group member and its contact call (Kondo et al., 2012), and grey parrots  
666 can visually and acoustically discriminate conspecifics (Giret et al., 2009). Therefore,  
667 maybe a concept of self could be cross-modal. In adult humans, priming experiments  
668 suggest that the brain processes information about the self in highly integrated ways: being  
669 exposed to one's own body odor and a visual or auditory presentation of one's name  
670 facilitated self-face recognition in a reaction time task (Platek et al., 2004). The perception  
671 of emotion through cross-modal sensory integration enables faster, more accurate and more  
672 reliable recognition (Yuval-Greenberg & Deouell, 2009). As mentioned before, matching-  
673 to-sample experiments using a bird's own odor, vocalizations and/or image can be used to  
674 study self-recognition. It would be interesting to present birds their own odor or  
675 vocalizations and see whether they facilitate mirror self-recognition, or to train them to  
676 give a particular response to their own image, and see whether priming effects would be  
677 found by presenting their odor or vocalization or names simultaneously. Of course, training  
678 birds to respond to their own vocalizations or odor and then priming them with other  
679 modalities could be done too. Such aspects and those linked to the formation of cross-  
680 modal individual recognition through experience and social interactions could be easily  
681 studied in captive populations of birds.

682 As in other animals, the concept of self in birds can be addressed through two main areas  
683 of research: self-referent phenotype matching and self-awareness.

684 Self-referent phenotype matching has been demonstrated in birds using visual stimuli and  
685 it is likely that it is at play when birds discriminate among different conspecifics based on  
686 acoustic cues. The major histocompatibility complex (MHC), which plays a central role in

687 disease resistance and immune defense, represents a special case of self-referent phenotype  
688 matching, and it is also involved in olfactory mate choice decision in several vertebrate  
689 taxa including birds (Caro et al., 2015).

690 Self-awareness is the most fascinating aspect of self-recognition information and it has  
691 been proposed to be an important component of the Theory of Mind. As mentioned before,  
692 most birds consider their own reflection as another individual. Corvids and parrots showed  
693 self-contingent behaviour in front of a mirror, but only magpies seem to recognize  
694 themselves in a mirror without extended exposure to the mirror or training (Prior et al.,  
695 2008).

696 The assumption that self-recognition is an indicator of self-awareness appears to be valid,  
697 since to show spontaneous self-recognition (without specific training), an animal needs to  
698 be sufficiently self-aware to understand how it looks from another perspective (Anderson  
699 & Gallup, 2015) and, as highlighted above, this ability is often correlated with other signs  
700 of self-awareness. On the other hand, the failure of an organism to respond appropriately  
701 to mirrors is more difficult to interpret and does not necessarily imply the absence of self-  
702 awareness (Povinelli, 1987). Therefore, birds may be self-aware, and show it in other  
703 experiments, without exhibiting MSR. First, the mirror test might not be appropriate for  
704 species that consider direct gaze as a threat such as dogs and many species of primates.  
705 Unlike primates, birds do not possess facial musculature revealing precise details about  
706 their emotional state. However, they can express some of their emotional states with their  
707 feathers, and, in birds that possess a crest such as the cockatoo, with their crest movements  
708 (Athan, 2010). Animals are usually tested alone but MSR could be obtained more rapidly

709 if animals were tested with another familiar individual. Indeed, simultaneous exposure to  
710 a familiar individual and its reflection in a mirror could facilitate MSR.

711 Second, one should keep in mind that though MSR reflects a crucial step in the emergence  
712 of self-recognition, the fully fledged capacity is complex, and comparative, clinical, and  
713 developmental studies suggest an overall gradual development of this capacity in animals  
714 including humans (Rochat, 2015). Behaviorists have tried to link MSR to conditioning,  
715 claiming that the relationship between self and mirror can be learned. As mentioned before,  
716 they successfully trained pigeons to locate a spot on the body by using a mirror (Epstein et  
717 al., 1981). In the same way, MSR was recently successfully induced in Rhesus monkeys  
718 after visual-somatosensory training. Monkeys were trained in front of a mirror to touch a  
719 light spot on their face produced by a laser light that elicited an irritant sensation. After 2-  
720 5 weeks of training, monkeys had learned to touch a face area marked by a non-irritant  
721 light spot or odorless dye in front of a mirror (Chang et al., 2015). These experiments do  
722 not really prove any self-awareness, however, since the critical issue is whether animals  
723 spontaneously connect their reflection with their own body. But it is worth mentioning that  
724 in studies performed with birds, mainly adult animals were used, without a precise  
725 knowledge of their developmental background although these aspects could be easily  
726 monitored in captive populations. Several studies have shown that animals including birds  
727 are often exposed to their own reflection for example in the drinking trough and  
728 manipulating this reflection can affect their behavior (Salzen & Cornell, 1968). Therefore,  
729 the duration of exposure to their own image is not really known, and mirror self-recognition  
730 may be linked to this duration.

731 In the same way that many bird species interpret their reflection in a mirror as a conspecific,  
732 it is likely that they consider playbacks of their BOS as a stranger's song and, as discussed  
733 above, this paradigm has been used extensively to study vocal interactions during territorial  
734 challenges (Akçay et al., 2011, 2013, 2014). However, even a chimpanzee touching a red  
735 spot on his head can be interpreted in different ways (Heyes, 1994), and reactions to  
736 playbacks of the animal's own vocalizations are even less easy to interpret in the context  
737 of self-recognition (Mc Arthur, 1987). For example, depending on the species, a bird would  
738 approach a speaker, produce songs and/or calls and/or remain silent. One possibility would  
739 be to use live or delayed auditory feedback. This could give the opportunity to the bird to  
740 adjust to the fact that vocalizations produced lived may sound distorted on playback.  
741 Moreover, if the animal was capable of auditory self-recognition, not only should it come  
742 to distinguish its vocalizations from those of other individuals, but it also ought to respond  
743 differentially to unexpected changes or distortions in the playback of its vocalizations that  
744 it did not itself produce, akin to the mark test of visual self-recognition (Suarez & Gallup,  
745 1987). Such experiments are challenging to conduct in the wild, but they would be easier  
746 to manage with captive populations of birds. In particular, to our knowledge, reactions of  
747 corvids or psittacids to the broadcast of their own vocalizations have never been  
748 investigated.

749 Studies obtained in oscine songbirds also emphasized the role of experience and  
750 development in the BOS recognition. In the case of the zebra finch that produces a short  
751 song, neural song replay during sleep has been interpreted as the bird 'dreaming' of his  
752 song (Dave & Margoliash, 2000). Such neural song replay could also be involved in the  
753 developmental learning process of this acoustic signal (Derégnaucourt et al., 2005).

754 To some extent, the voice could be considered as an embodiment of self social contexts,  
755 and developmental changes in the voice patterns might enhance the development of  
756 consciousness and self-awareness in humans and probably also in other animals. The  
757 acoustic parameters of the vocalizations could provide information about personal identity  
758 but it could also inform about the internal state of the producer. Like in mammals, stress  
759 can induce vocal changes in the vocalizations of birds. For example, in the zebra finch,  
760 acoustic parameters of the contact calls are modified following the injection of  
761 corticosterone, considered a stress hormone (Perez et al., 2012). Playback experiments  
762 have shown that finches can perceive acoustic differences between stressed and non-  
763 stressed contact calls. Moreover, in breeding pairs, playback of stressed contact calls from  
764 the sexual partner induces an increase of corticosterone (Perez et al., 2015). Also, we do  
765 not know to what extent the vocalizations can be transformed without losing information  
766 such as the coding of individuality or the emotional content.

767 The role of experience is also important in the context of vocal labeling shown in several  
768 species of parrots. The representational use of learned identity labels represents an  
769 interesting parallel to humans and the apparent necessity for these vocal labels in  
770 maintaining group cohesion may lie at the root of the evolution of complex communication  
771 and cognition systems. Experiments in spectacled parrotlets have suggested that these birds  
772 have a mental representation of at least their family members because they use different  
773 labels for them (Wanker et al., 2005). In this domain, many interesting questions still  
774 remain unanswered: how would a bird react when the vocal label (call of a family member)  
775 is produced? Would it affect his behavior if this familiar individual was absent or present?

776 Field studies provide interesting tracks for future research in this domain. As previously  
777 mentioned, some experiments with broadcast of the BOS in the male's territory suggest  
778 that its reactions could be affected by the reaction of its neighbors (Brooks & Falls, 1975).  
779 Taking advantage of recent technological developments that enable both the vocal (Ter  
780 Maat et al., 2014) and spatial (Farine et al., 2015) tracking of different individuals in a  
781 social network, it would be of interest to monitor not only the behavior of a target individual  
782 during song broadcast in its territory but also those of its different neighbors.  
783 Finally, knowing more about sentience and awareness in animals could influence our  
784 decisions about our obligations to them (Broom, 2010). Several species of birds are raised  
785 in both poultry farms for meat and egg production, and research facilities. Self-  
786 consciousness matters from an ethical point of view since it can give rise to forms of  
787 suffering above the immediate sensations of pain or distress, although understanding and  
788 improving animal welfare can be approached without considering animal consciousness  
789 (Dawkins, 2012). Thus, the perception of self has numerous implications for basic research,  
790 but it may also be important for animal welfare and legislation.  
791

792

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1266

1267 **Table legend**

1268

1269 **Table 1. List of species that were tested with the Mirror Self Recognition Paradigm.**

1270 We did not include primates in this table because the literature relative to them is very

1271 abundant and the present paper focuses on birds. The current consensus concerning

1272 primates is that great apes pass the mark test, whereas monkeys do not pass that test,

1273 although they may do it after extensive training (for reviews, see for example Anderson &

1274 Gallup, 2011, 2015; Suddendorf and Butler, 2013).

1275

1276 **Legends of figures**

1277

1278 **Figure 1. Avian and mammalian brains contain homologous structures and similar**

1279 **functional circuitry.**(a) Midline sagittal section of a human brain showing major

1280 structures, including those involved in generating conscious states (e.g. cortex, thalamus,

1281 and basal ganglia).(b) Midline sagittal section of the brain of a zebra finch, a songbird.

1282 Major neural structures are shown, including those with mammalian homologs. Also

1283 shown is a greatly simplified schematic of the anterior forebrain pathway for song learning

1284 (yellow arrows) involving components of the basal ganglia, including the striatal nucleus

1285 Area X ('X' in filled red circle). The circular inset to right of human brain shows zebra

1286 finch brain to scale for comparison. Adapted from Edelman & Seth, Trends in

1287 Neurosciences 2009.

1288

1289 **Figure 2. Relative brain size across birds and mammals.** Graphs displaying the

1290 relationship between (log) body weight and (log) brain volume across various birds and

1291 mammals (e.g. corvids, parrots, apes, dolphins, Australopithecus and modern Homo

1292 sapiens, pigeons and rats. Adapted from Van Horik & Emery, Wiley Interdisciplinary

1293 Reviews: Cognitive Science 2011.

1294

1295 **Figure 3. Adapted version of the mark test developed by Gordon Gallup with magpies**

1296 (*Pica pica*). (A) Attempt to reach the mark with the beak; (B) touching the mark area with

1297 the foot; (C) touching the breast region outside the marked area; (D) touching other parts

1298 of the body. Behaviours (A) and (B) entered the analysis as mark-directed behaviour;

1299 behaviours (C) and (D) and similar actions towards other parts of the body were considered  
1300 self-directed, but not related to the mark. Adapted from Prior et al., PLoS Biology 2008.

1301

1302 **Figure 4. Schematic representation of the avian song control system and its auditory**

1303 **inputs.** The avian song system can be divided into three main divisions. The descending  
1304 motor pathway (shown in black) includes telencephalic areas HVC and RA as well as  
1305 brainstem nuclei that drive the muscles of the syrinx (nXIIts) or the respiratory system  
1306 (Ram and PAm). These later two structures form part of a vocal respiratory network that  
1307 also includes DM. The second division, sometimes called the ventral motor pathway,  
1308 consists of projections from the diencephalon and brainstem back to HVC (shown in  
1309 green). The third major division of the song system consists of the anterior pathway (shown  
1310 in light red), which is made up of Area X, DLM, and LMAN. The song system receives  
1311 processed auditory information from an ascending auditory pathway (shown in blue).

1312 Areas where BOS-selective responses have been recorded are outlined in red. Anatomical  
1313 names: DLM, medial part of the dorsolateral thalamic nucleus; LMAN, lateral  
1314 magnocellular nucleus of the anterior nidopallium; Field L is the primary auditory  
1315 forebrain structure in birds; Area X, Area X of the medial striatum; Nif, nucleus  
1316 interfacialis of the nidopallium; RAm, nucleus retroambigualis; PAm, nucleus  
1317 paraambigualus; DM, dorsomedial nucleus of the intercollicular complex; CMM, caudal  
1318 medial mesopallium; CLM, caudal lateral mesopallium; Field L, auditory forebrain areas  
1319 consisting of Field L1, L2, L2a, L2b and L3; Ov/Ovm, nucleus ovoidalis; MLd, dorsal  
1320 lateral nucleus of the mesencephalon; NCM, caudal medial nidopallium; LLV, ventral

1321 nucleus of the lateral lemniscus; EXP, expiration; INSP, inspiration. Adapted from  
1322 Margoliash & Schmidt, Brain & Language 2010.

1323

1324 **Figure 5. Vocal labelling in spectacled parrotlets (*Forpus conspicillatus*).** Spectrograms  
1325 of contact calls from the male Eddi interacting with different partners. (a, d, g) Eddi  
1326 interacting with his pair mate Renee, (b, e, h) Eddi interacting with his offspring Ustinov  
1327 and (c, f, i) Eddi interacting with his offspring Uvo. (Fast Fourier Transformation (FFT)  
1328 window size: 256 pts; frequency resolution: 125 Hz; time resolution: 8.0 ms; number of  
1329 FFTs: 500 steps). Adapted from Wanker et al., Animal Behaviour 2005.