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The perception of self in birds

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Abstract:

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

1. Introduction

1.1. The Concept of Self: definitions

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

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

As underlined by Bekoff & Sherman (2004) such self-referencing can be reflexive and non-cognitive. These authors suggest two other degrees of self-cognizance: (1) self-awareness, that enables an individual to discriminate consciously or subconsciously between its own body or possessions from those of others, and (2) self-consciousness, which involves having a sense of one's own body as a named self, and thinking about one's self and one’s own behavior in relation to the actions of others. According to Bekoff & Sherman (2014), self-awareness does not imply that individuals use self-referent phenotype matching or vice versa, whereas self-consciousness implies that an individual is self-aware, and that it can use self-referencing. Therefore, self-referent phenotype matching is probably a prerequisite for self-consciousness. However, other researchers do not make the same distinction between self-awareness and self-consciousness and these two expressions are often used with the same significance. For example, Lewis (2011) defines self-awareness as “a mental representation of me.”

1.2. Mirror Self-Recognition

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

In humans, MSR does not emerge until 15-24 months of age (Amsterdam, 1972; Lewis, 2011) when the first signs of self-awareness appear: these include introspection and mental state attribution (Piaget, 1952) along with empathy (Bischof-Kohler, 2012), the use of personal pronouns and pretend play (Lewis & Ramsay, 2004). Apart from humans, strong evidence of MSR have been obtained only for the four great apes (Anderson & Gallup, 2011), bottlenose dolphins (*Tursiops truncatus*; Reiss & Marino, 2001), Asian elephants (*Elephas maximus*; Plotnik et al., 2006) and magpies (*Pica pica*; Prior et al., 2008). A variety of organisms including fishes, birds, sea lions, dogs and cats, although they have not been formerly tested with the mirror mark test, produce very different behaviors toward their own reflections (Parker et al., 1994). Several species persist in responding to mirrors as if confronted by another conspecific, even in the case of years of continuous exposure to mirrors (Suarez & Gallup, 1986). Mirrors induce socially meaningful and strong responses with such reliability that mirror-image stimulation has been extensively employed to study aggressive and social patterns in a wide variety of species from fishes to mammals (Parker et al., 1994). Some of these species demonstrate the ability to use a mirror to mediate or guide their behavior, for example macaques (*Macaca fuscata*) can use a mirror to reach hidden food that is only visible with a mirror (Itakura, 1987). However, the conclusion that self-directed behavior in response to a mirror implies some form of human-like self-awareness is not free from controversy (Parker et al., 1994). Similarly, implication of self-recognition when passing the mark test is also a subject of debate (Medina et al., 2011; Suddendorf & Butler, 2013).

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

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

1.3. Why study the perception of self in birds?

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

Several experiments and observations in birds have indirectly shown that the perception of self is particularly relevant during interactions with other individuals, especially in the context of sexual selection. Monogamy is particularly widespread in birds and several species exhibit assortative pairing: pairing with an individual of similar quality or geographical origin. For example, non-random mating with respect to coloration is commonly observed in birds (Hill, 2006). In domesticated budgerigars (*Melopsittacus undulatus*), females prefer potential mates with contact calls more similar to their own (Moravec et al., 2010). In the laboratory, Holveck and Riebel (2009) observed that female zebra finches (*Taeniopygia guttata*) reared in poor conditions develop acoustic preferences for the songs of males reared in similar conditions. Several experiments have also shown that females reduce their choosiness when their body condition is experimentally compromised (Burley & Foster, 2006; Lerch et al., 2011, 2013). For example, cutting the flight feathers of female canaries (*Serinus canaria*) decreases female choosiness towards male songs. The authors propose that this decrease in choosiness is likely to be a residual behavioral adaptation of being in poor conditions and it follows the evaluation of their own flight quality in the aviary and therefore results from the perception of self-properties (Lerch et al., 2013).

The perception of self can also be affected by the experience of the animals. Some species have the possibility to modify their self-characteristics through learning, and this is particularly well-documented in some bird species in the vocal domain (Bolhuis et al., 2010; Bradbury & Balsby, 2016). Like humans, oscine songbirds, parrots and hummingbirds exhibit vocal production learning, the capacity to imitate sounds from their environment, mainly those produced by conspecifics. This ability which is a prerequisite for the development of human speech, is a rare trait in the animal kingdom and is shared with certain marine mammals, elephants and bats but seems to be absent in non-human primates (Bolhuis et al., 2010), although some vocal plasticity and abilities for vocal social learning have recently been demonstrated in monkeys (Lemasson et al, 2005; Takahashi et al., 2015). The architecture and connectivity of avian and mammalian brains are much more similar than had been recognized previously (Reiner et al., 2004). For instance, avian pallial ‘song’ regions bear functional similarities with human auditory and motor cortices and the importance of the basal ganglia for both speech and birdsong is starting to be understood mechanistically (Doupe et al., 2005; Jarvis et al., 2005; Mooney, 2009). These aspects and others consolidate birdsong as the biological model of choice to study the behavioral, molecular and cellular substrates of vocal learning, an important component of language acquisition (Bolhuis et al., 2010). Studies that cannot be conducted on humans for obvious ethical reasons can easily be done with captive populations of oscine songbirds, and exposing a bird to its own song is a useful method to investigate the neural substrates for individual recognition. Here, we are not reviewing the literature dealing with exposure to self-produced vocalizations in mammals, but it is likely that the number of studies would be greatly outnumbered by those conducted in birds.

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

This high degree of evolutionary convergence is especially apparent in the cognitive abilities of corvids and parrots, big-brained birds whose forebrains have a relative size the same as those of apes, and who behaviorally perform at a comparable level with apes in many domains such as episodic memory, tool-use and theory of mind (Figure 2; Emery & Clayton, 2004; Emery, 2006; Güntürkün & Bugnyar, 2016; Van Horik & Emery, 2011). In the field of animal cognition, variants of the mirror test have been used in birds but so far only magpies have been shown to recognize their own reflection (Prior et al., 2008). We will discuss this result later.

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

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

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

Finally, playback of birds’ own vocalizations have been extensively used both in the field and in the laboratory and in many species of birds. Oscine songbirds exhibit an especially strong response to the broadcast of their own song, both at the behavioral and at the neural levels. Such experiments have helped us decipher the mechanisms of vocal coding/decoding for example during socio-sexual interactions such as territory defense. Exposing a bird to its own vocal signature is a useful means to investigate the neural substrates of individual recognition; a fruitful topic of research that has been barely addressed in other sensory modalities. This topic has been also barely addressed in mammals.

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

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

2. Visual representations

2.1. Self-referent visual phenotype matching

Most birds learn conspecific characteristics from their parents and siblings. They probably also take into account their own phenotype, and later match features of encountered individuals to that template through self-referent phenotype matching. Such self-referencing was studied with cross-fostered and naïve (raised in social isolation) chicks (*Gallus domesticus*, Salzen & Cornell, 1968; Vidal, 1975). Salzen and Cornell (1968) conducted a series of experiments to test the hypothesis that self-perception explains preferential choices of conspecifics by birds raised in isolation. They painted chicks with different colors and kept them in social isolation for 8 days before testing them in a 2-choice experiment with a companion from the same color and another one with a different color. The authors conclude that the self-perception hypothesis is tenable at least if perception through reflection in water is included. Indeed, chicks reared in isolation with no drinking trough (water was administered by pipette directly in the crop) failed to show any tendency to choose a companion with their own color (Salzen & Cornell, 1968). Even with modifications to prevent self-reflection in water such as painting the bottom of drinking trough in white (Vidal, 1975), there is evidence that birds can perceive their shadow. For example, domestic roosters exhibit courtship displays towards their shadow (Vidal, 1975). Vidal (1975) observed that an isolated cock perceived and fixated on parts of its own body (self-fixation), but remained able to orient and adjust its behavior towards a partner resembling itself. Social isolation cannot prevent proprioceptive feedback that can complete the visual information that an animal cannot assess without a mirror (Vidal, 1975). It has been acknowledged for a long time that experimentally isolated animals are indeed never isolated from themselves (Lehrman, 1953).

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

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

Mirror-induced self-directed behavior has been studied in several species of birds. Most of the species tested so far failed to show self-directed behavior in front of their mirror-image. They have been tested either in the wild (chickadees *Parus atricapillus*, Censky & Ficken, 1982; glaucous-winged gulls *Larus glaucescens*, Stout et al., 1969) or in the laboratory in captivity (Blue grouse *Dendragapus obscurus*, Stirling, 1968; budgerigars *Melopsittacus undulatus* and house sparrows *Passer domesticus*, Gallup & Capper, 1970; a kea *Nestor notabilis*, Diamond & Bond, 1989; zebra finches *Taeniopygia guttata*, Ryan 1978; cedar waxwings *Bombycilla cedrorum* and Juncos *Junco hyemalis*, Andrews, 1966; Lovebirds *Agapornis roseicollis*, Delsaut & Roy, 1980; African Grey Parrot *Psittacus erithacus*: Pepperberg et al., 1995; Jungle Crow *Corvus macrorhynchos*: Kusuyama et al., 2000; Java *Sparrow Padda oryzivora*: Watanabe, 2002; New Caledonian Crow *Corvus moneduloides:* Medina et al., 2011; Jackdaw *Corvus monedula*: Soler et al., 2014). Many of them respond to thei self-image with social behaviour, i.e. treating the mirror-image as if it were a conspecific. Some bird species exhibit aggressive behavior in the presence of a mirror while others exhibit courtship displays. A Flamingo (*Phoeniconais minor*) flock exhibited marching displays in front of mirrors (Pickering & Duverge, 1992). Some bird species such as house sparrows, parakeets and zebra finches exhibit a preference for mirror image stimulation over visual access to a conspecific (Gallup & Capper, 1970; Ryan, 1978). This preference was shown in the absence of auditory cues. The authors hypothesized that the mirror image could be perceived as a supernormal stimulus since the mirror image would always be both predictable and compatible with the animal’s behavior. Mirrors are often used as a social substitute to reduce stress in highly social birds, such as starlings (*Sturnus vulgaris*, Henry et al., 2008) and zebra finches, kept in social isolation for laboratory experiments. Female pigeons (*Columba livia*) would ovulate when exposed to her own reflection in a mirror (Matthews, 1939). It is noteworthy that the length of exposure and size of the mirror vary greatly across these studies. So far, MSR capacity using an adapted version of the experimental procedure developed by Gallup (1970) has been found only in one bird species, the magpie (Prior et al., 2008; Figure 3). The authors used a sticker as a mark that was stuck under the beak, in the throat area, outside the magpies' visual field. Two magpies out of five were capable of removing the sticker by scratching with their foot in mirror-present sessions. The results obtained in magpies have important biological and cognitive implications because the fact that magpies were able to pass the mark test means that mirror self-recognition evolved independently in the magpie and great apes (which diverged 300 million years ago) and that the neocortex (which is not present in the bird's brains as mentioned before) is not a prerequisite for MSR as previously believed (Prior et al., 2008). Using the same experimental procedure, Soler and colleagues (2014) failed to show MSR in jackdaws: they showed mark-directed behavior in the mirror but also in the no-mirror condition. Moreover, the authors pointed out potential methodological problems with the study on magpies. According to them, magpies might have detected the sticker using tactile sense through feather sensitivity. They suggest to use more appropriate marking methods for future avian marking tests such as using paint that does not agglomerate the feathers or, at least allows for the perfect separation of feathers when dried, for instance typing correction fluid. However, as two of the magpies showed significantly more mark-directed behavior when tested in front of a mirror than in the absence of a mirror, tactile sense cannot be the sole explanation for their mark-directed behavior. Another interesting result from the magpie and the jackdaw studies is that in both experiments the birds showed self-contingent behavior (i.e., they moved their head or the whole body back and forth in front of the mirror in a systematic way). In the magpie study, the 3 birds that showed self-contingency behavior also showed mark-directed enhanced behavior in the mark test (this was significant for two of them).

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

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

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

It is extremely crucial to check whether self-directed behavior in birds represents a spontaneous response to seeing their own body in the mirror. Pigeons were successfully trained to peck at a spot on their bodies that could only be seen with the aid of a mirror (Epstein et al., 1981). Thompson & Contie (1994) failed to replicate these results although the exact details of the training procedure had not been documented and training could have been a crucial factor in obtaining positive results. Indeed, Uchino and Watanabe (2014) recently revisited self-recognition in pigeons using a similar procedure as Epstein and collaborators. They observed that after extensive training with food reinforcement, two pigeons spontaneously integrated the learned self-directed and mirror-use behavior and displayed self-directed behavior in a mark test. In a previous experiment, the authors trained pigeons to respond to live video images of themselves and not to respond when they viewed prerecorded videos (Toda & Watanabe, 2008). Pigeons' discrimination of self-movies was based on the temporal contiguity between their behavior and visual feedback since their relative response rate to delayed presentation of live self-movies gradually decreased as the temporal discrepancy between their own behavior and the corresponding video increased (Toda & Watanabe, 2008). These results suggest that the visual properties of self-image are not the primary cue for self-recognition, and the visual-proprioceptive contingency between a subject's action and the corresponding visual scene reflected in a mirror might be an essential component. If so, subjects might not require complex cognitive and social abilities to discriminate self from others (Toda & Watanabe, 2008). That said, pigeons need extensive training for this form of self-recognition which contrasts drastically with humans and other species that do not need such training. This is the case with the magpies that exhibited self-related behavior in front of a mirror after a rather short cumulative exposure time and without being specifically trained to do so (Prior et al., 2008).

3. Exposure of a bird to its own smell

In several petrel species of burrow nesters, the burrow olfactory signature is important for homing. Using a T-maze experiment, de Léon et al. (2003) showed that European storm petrel chicks (*Hydrobates pelagicus*) are able to recognize their own odor and that this odor leads them back to the nest.

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

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

As discussed above, some birds can recognize their own odor, but this could be based on a simple familiarity rather than on a concept of self. To separate between these alternatives is not easy. Some matching-to-sample experiments could be conducted in which a bird would have to match the odor of different conspecifics, including itself, to vocalizations or images. However, to solve this task, the bird would have to identify his own odor but also his own vocalizations or image. Some priming experiments (exposure to one stimulus to influence the response to another stimulus) using different modalities could also be informative in this respect.

4. Exposure of a bird to its own vocalizations

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

4.1. Experiments in the wild

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

In some species, behavioral responses to song playbacks are maximal when the song broadcast is the BOS. For example, in great tits (Falls et al., 1982), western meadowlarks (*Sturnella neglecta*; Falls, 1985) and song sparrows (Stoddard et al., 1992), song matching was maximal following broadcast of the BOS in comparison with neighbor and stranger songs. In other studies, the BOS produced an intermediate response strength falling between that elicited by the songs neighbors and strangers (ovenbirds *Seirus aurocapillus*: Weeden & Falls, 1959; white-throated sparrow *Zonotrichia alhicollis*: Brooks & Falls, 1975; swamp sparrows *Melospiza georgiana*: Searcy et al., 1981; red-winged blackbirds *Agelaius phoeniceus*: Yasukawa et al. 1982).The majority of birdsong research concerns male song, but females from many oscine songbird species also sing (Odom et al., 2014). In the red-winged blackbird, females gave statistically similar responses to playback of BOS and stranger songs (Beletsky, 1983).

In song sparrows, results differ between different studies and this highlights the necessity to take into account the methodological aspects of the playback procedure, the response measures and the statistical treatment of the data. Some studies have shown that the response of male song sparrows to the BOS is not different than the response to a stranger song, both in terms of aggression (approach to the speaker; Searcy et al., 1981) and song matching (Stoddard et al., 1992). In contrast, in the only study conducted with the goal to demonstrate auditory self-awareness in birds, Mc Arthur (1986) observed that the territorial response was minimal during the broadcast of the BOS and that the strength of the territorial response was inversely correlated with the similarity of the stimulus song to the BOS. Nevertheless, song matching was also higher for the BOS than for a stranger song acoustically dissimilar to the BOS. Some of these results were not statistically significant. It is also worth mentioning that these studies were done before the advent of the multivariate-measure approach (such as principal component analysis) that became a standard in the design of playback experiments since the 90's (Mc Gregor, 1992).

How can we interpret these results? In the case when the bird exhibits a strong response, it may be that he perceived the BOS as a fully shared stranger song. One's own sounds might be perceived as different since the normal bone conduction that is present when emitting a sound is absent from the playback sound. In the same way the human voice sounds strange when heard from a tape, a bird could react to his BOS as though it were produced by a stranger. Response to BOS in song sparrows is similar to response to stranger song both in terms of matching (Stoddard et al. 1992) and aggression (Searcy et al. 1981 but see Mc Arthur, 1986), and another study suggest that there is no voice recognition in this species (Beecher et al., 1994). However, a bird could also recognize his BOS and react strongly because he is surprised to hear himself. He would approach the loudspeaker or even sing in order to investigate what is happening; therefore, very detailed description of the bird's behaviors would be needed to discriminate between a purely territorial response and a surprised response.

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

Brooks and Falls (1975) provide an explanation for an intermediate response to the playback of BOS (responses measuring between those to stranger and to neighbor songs). During the broadcast of a song in the territory of a focal bird, song activity from his neighbors is sometimes observed and this vocal activity could affect the behavioral response of the focal bird. During the broadcast of a stranger song, the strong response of a focal bird could be enhanced by the strong response of his neighbors. During the broadcast of his BOS, his neighbors should recognize him and act accordingly by singing less. This low activity might affect the response of the focal bird. But the BOS may also sound intermediate in terms in familiarity: less familiar than a neighbor song because of the bone distortion, but more familiar than a completely stranger song.

The different reactions to the BOS playback are also probably linked to the different socio-ecological aspects of the different species that were tested. During song playback, males of some species engage in counter-singing: they produce the song that best resembles the playback song (Bremond, 1968; Falls et al., 1988). Indeed, many species of oscine songbirds often engage in copying and matching sounds through which they address each other. Depending on the context, they could use either song type matching, (producing the same song they hear) or repertoire matching (producing a shared song type while avoiding singing the same song type). Playback of the BOS have been used extensively in several experiments on matching in song sparrows (Akçay et al., 2011, 2013, 2014; Anderson et al. 2005; Searcy et al., 2013; Stoddard et al., 1992). For example, song sparrows use song type matching when defending their territory against an unknown male, but avoid it when interacting with known neighbors with whom they use more subtle repertoire matching (Beecher & Campbell, 2005). Repertoire matching may allow addressing a neighbor in a more affiliative or neutral way. For example, song sparrows, western meadowlarks and great tits do not type-match a neighbor’s song but do the BOS or a stranger’s song (Falls, 1985; Falls et al., 1982; Stoddard et al., 1992). In some species such as the great tit, if the theme broadcast is absent from the bird’s repertoire, it will reply with the theme closest in structure within its own repertoire (Krebs et al., 1981). This form of categorization suggests that there is an auditory reference to which the stimulus is compared before production occurs. Such a reference is the result of different influences, particularly learning. More recently, playback of the BOS brought to light a turnover in repertoire composition over a relatively short period in great tits (Franco & Slabbekoorn, 2009).

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

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

4.2. Experiments in the laboratory

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

Similarly, adult zebra finches (*Taeniopygia guttata*) express a robust behavioral preference for the playback of their BOS compared with conspecific male song in a phonotaxis experiment (Remage-Healey et al., 2010). However, the tutor song is a stronger stimulus than the BOS: finches exposed either passively or through operant conditioning to the tutor song during development preferred the training song over a novel song as well as over their BOS as adults (Adret, 1993). Using operant conditioning, it was shown that males trained to discriminate between their own song and another song from their aviary reached criterion in a fewer number of trials than males that had to discriminate between songs from their own aviary, with the most training required by males discriminating between songs they had not heard before (Cynx & Nottebohm, 1992). While most studies investigated songs in oscine songbirds, it is worth mentioning that the 'autogenous reference' could be also used in non-vocal learner species through self-referent phenotype matching. For example, in a two-choice experiment, neonate chicks (*Gallus domesticus*) exhibited a preference for a speaker broadcasting a maternal call with acoustic features resembling those of the bird's own twitter rather than a speaker broadcasting a maternal call with acoustics dissimilar to their own twitter (Guyomarc'h, 1973). Similarly, chicks raised in mixed flocks of two varieties, when tested in a Y-maze, learn to go to chicks of their own variety more readily than to those of the other variety (Howells & Vine, 1940). Besides genetic influences, it is also plausible that the chick's experience with its own chirping could be used as a source of differential learning (Schneirla, 1946).

At the neural level, the earliest attempts to record singing-related activity in the brain of freely behaving oscine songbirds (canaries and white-crowned sparrows) detected increased activity not only during singing but also when the BOS was broadcast through a speaker (Mc Casland & Konishi, 1981). This paradigm, used in more than one hundred studies so far, could permit to look for the neural template that determines the BOS.

Songbirds have specialized, discrete brain regions for song production and learning (Figure 4). The Song Motor Pathway (SMP) is involved in song production and certain aspects of song learning, and the Anterior Forebrain Pathway (AFP) that connects with the motor pathway, is essential for sensorimotor learning and adult song plasticity. These two pathways together are usually called the ‘song control system’ (Brainard & Doupe, 2002). The sensorimotor nucleus HVC (used as a proper name) which belongs to the SMP was the first song nucleus in which song-selective neurons were observed (Mc Casland & Konishi, 1981). Most neurons from the HVC that are responsive to song playback are highly selective for the BOS, firing more to forward auditory playback of the BOS than to reverse BOS or conspecific songs (Margoliash, 1983, 1986; Margoliash & Konishi, 1985; Mooney, 2000).

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

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

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

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

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

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

Taken together, these results suggest that BOS-selective neurons in oscine songbirds could provide an ‘error signal’ that promotes changes in song production when a mismatch is detected between auditory feedback from self-song and the memorized song template, and could thus have a role in both song learning and maintenance (but see Leonardo, 2004). A second function might be the perception of conspecific song. These functions are not necessarily mutually incompatible. They could also be at play in non-songbird species. For example, the influence of auditory feedback on sexual development has also been extensively studied in a non-vocal learner species, the ring dove (*Streptopelia risoria*). In this species, courtship is initiated by males. Males' coos (the equivalent of song in oscine songbirds) is an integral feature of the courtship. When the female is motivated, she produces her own 'nest coos' in response to the male's coos. Several experiments in intact, muted, and deafened female doves have shown that a female's own nest coos affect her endocrine state (Cheng & Durand, 2004). For example, playback of the female's own coos was the most effective stimulus for her follicular development, but playback of other female coos was also more effective than playback of male song.

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

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

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

5. Use of learned signals as individually specific labels

It is well known, in both vocal and non-vocal learners that animals can recognize a conspecific based on acoustic cues. Addressing of specific individuals in a communication network can be achieved by vocal labeling, where a specific vocalization is linked to a specific individual (Balsby et al., 2012). In captivity, animals can be easily trained to associate a sound, often a human spoken word, with a personal reward such as food or care. For example, using a combination of classical and operant conditioning procedures, pigs living in a group can be trained to enter a feeder only after an individual acoustic signal has been presented. This call feeding procedure minimizes queuing and thereby reduces aggression, stress and injuries associated with feeding (Manteuffel et al., 2011). In the wild, there is evidence that bottlenose dolphins recognize their own vocal signature (King & Janik, 2013). In birds, some species of parrots have been found capable of using arbitrary, learned signals to label or name objects in experimental studies (Pepperberg, 1981). In captivity, parrots can learn to pronounce their own name and to respond to it more than to the name of other individuals (Bovet, Giret & Péron, unpublished obs.), but, as in the case of pigs cited above, this could be the result of a simple conditioning effect that is not necessarily linked to self-awareness. Researchers working with ravens (*Corvus corax*) can also easily get the bird’s attention by calling its name (Bugnyar et al., 2016). One raven raised in captivity in isolation who was named Goliath would produce its name when his caretaker would enter in the room (Gwinner, 1964). There is also evidence that a kind of naming is also present in the natural communication system of some bird species. For example, spectacled parrotlets (*Forpus conspicillatus*) use contact calls to refer to a social companion and thus label or ‘name’ their conspecifics (Wanker et al., 2005; Figure 5). Such labelling could help capturing the attention of and further interaction with a particular individual in the social group, similarly to humans calling out the name of an associate at a noisy social gathering. It is possible that these contact calls used as labels or ‘names’ could be imitations of the addressee’s calls but that hypothesis has not been tested yet in this species (Bradbury & Balsby, 2016). Such imitation have been observed in orange-fronted conures (*Aratinga canicularis*). Conures can imitate contact calls almost immediately upon hearing them (Balsby & Bradbury, 2009). In this fusion/fission species that is non-territorial and that lives in small groups, vocal matching is observed in the wild prior to flock fusion and might represent some form of negotiation (Balsby & Bradbury, 2009). Orange-fronted conures can use imitation of contact calls to address specific individuals of a flock (Balsby et al., 2012). The authors argue that the fission-fusion flock dynamics of many parrot species has been an important factor in evolving conures’ and other parrots’ exceptional ability to imitate (Bradbury & Balsby, 2012).

6. Conclusion and future directions

Exposing an animal to its own image, smell or vocalizations experimentally has helped us understand how individuals process social information. Since the perception of self can be achieved using different sensory modalities, it would be of interest to investigate whether each modality controls a different level of self or if these different levels are linked to each other in order for an individual to build an integrative and unified template of self. In many species, subjects are able to match the voice of a familiar conspecific to its image. For example, large-billed crows are sensitive to identity congruence between the visual presentation of a group member and its contact call (Kondo et al., 2012), and grey parrots can visually and acoustically discriminate conspecifics (Giret et al., 2009). Therefore, maybe a concept of self could be cross-modal. In adult humans, priming experiments suggest that the brain processes information about the self in highly integrated ways: being exposed to one’s own body odor and a visual or auditory presentation of one’s name facilitated self-face recognition in a reaction time task (Platek et al., 2004). The perception of emotion through cross-modal sensory integration enables faster, more accurate and more reliable recognition (Yuval-Greenberg & Deouell, 2009). As mentioned before, matching-to-sample experiments using a bird’s own odor, vocalizations and/or image can be used to study self-recognition. It would be interesting to present birds their own odor or vocalizations and see whether they facilitate mirror self-recognition, or to train them to give a particular response to their own image,and see whether priming effects would be found by presenting their odor or vocalization or names simultaneously. Of course, training birds to respond to their own vocalizations or odor and then priming them with other modalities could be done too. Such aspects and those linked to the formation of cross-modal individual recognition through experience and social interactions could be easily studied in captive populations of birds.

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

Self-referent phenotype matching has been demonstrated in birds using visual stimuli and it is likely that it is at play when birds discriminate among different conspecifics based on acoustic cues. The major histocompatibility complex (MHC), which plays a central role in disease resistance and immune defense, represents a special case of self-referent phenotype matching, and it is also involved in olfactory mate choice decision in several vertebrate taxa including birds (Caro et al., 2015).

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

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

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

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

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

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

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

Field studies provide interesting tracks for future research in this domain. As previously mentioned, some experiments with broadcast of the BOS in the male’s territory suggest that its reactions could be affected by the reaction of its neighbors (Brooks & Falls, 1975). Taking advantage of recent technological developments that enable both the vocal (Ter Maat et al., 2014) and spatial (Farine et al., 2015) tracking of different individuals in a social network, it would be of interest to monitor not only the behavior of a target individual during song broadcast in its territory but also those of its different neighbors.

Finally, knowing more about sentience and awareness in animals could influence our decisions about our obligations to them (Broom, 2010). Several species of birds are raised in both poultry farms for meat and egg production, and research facilities. Self-consciousness matters from an ethical point of view since it can give rise to forms of suffering above the immediate sensations of pain or distress, although understanding and improving animal welfare can be approached without considering animal consciousness (Dawkins, 2012). Thus, the perception of self has numerous implications for basic research, but it may also be important for animal welfare and legislation.

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Table legend

Table 1. List of species that were tested with the Mirror Self Recognition Paradigm. We did not include primates in this table because the literature relative to them is very abundant and the present paper focuses on birds. The current consensus concerning primates is that great apes pass the mark test, whereas monkeys do not pass that test, although they may do it after extensive training (for reviews, see for example Anderson & Gallup, 2011, 2015; Suddendorf and Butler, 2013).

Legends of figures

Figure 1. Avian and mammalian brains contain homologous structures and similar functional circuitry.(a) Midline sagittal section of a human brain showing major structures, including those involved in generating conscious states (e.g. cortex, thalamus, and basal ganglia).(b) Midline sagittal section of the brain of a zebra finch, a songbird. Major neural structures are shown, including those with mammalian homologs. Also shown is a greatly simplified schematic of the anterior forebrain pathway for song learning (yellow arrows) involving components of the basal ganglia, including the striatal nucleus Area X ('X' in filled red circle). The circular inset to right of human brain shows zebra finch brain to scale for comparison. Adapted from Edelman & Seth, Trends in Neurosciences 2009.

Figure 2. Relative brain size across birds and mammals. Graphs displaying the relationship between (log) body weight and (log) brain volume acroos various birds and mammals (e.g. corvids, parrots, apes, dolphins, Australopithecus and modern Homo sapiens, pigeons and rats. Adapted from Van Horik & Emery, Wiley Interdisciplinary Reviews: Cognitive Science 2011.

Figure 3. Adapted version of the mark test developed by Gordon Gallup with magpies (*Pica pica*). (A) Attempt to reach the mark with the beak; (B) touching the mark area with the foot; (C) touching the breast region outside the marked area; (D) touching other parts of the body. Behaviours (A) and (B) entered the analysis as mark-directed behaviour;

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

Figure 4. Schematic representation of the avian song control system and its auditory inputs. The avian song system can be divided into three main divisions. The descending motor pathway (shown in black) includes telencephalic areas HVC and RA as well as brainstem nuclei that drive the muscles of the syrinx (nXIIts) or the respiratory system (Ram and PAm). These later two structures form part of a vocal respiratory network that also includes DM. The second division, sometimes called the ventral motor pathway, consists of projections from the diencephalon and brainstem back to HVC (shown in green). The third major division of the song system consists of the anterior pathway (shown in light red), which is made up of Area X, DLM, and LMAN. The song system receives processed auditory information from an ascending auditory pathway (shown in blue). Areas where BOS-selective responses have been recorded are outlined in red. Anatomical names: DLM, medial part of the dorsolateral thalamic nucleus; LMAN, lateral magnocellular nucleus of the anterior nidopallium; Field L is the primary auditory forebrain structure in birds; Area X, Area X of the medial striatum; NIf, nucleus interfacialis of the nidopallium; RAm, nucleus retroambigualis; PAm, nucleus paraambigualus; DM, dorsomedial nucleus of the intercollicular complex; CMM, caudal medial mesopallium; CLM, caudal lateral mesopallium; Field L, auditory forebrain areas consisting of Field L1, L2, L2a, L2b and L3; Ov/Ovm, nucleus ovoidalis; MLd, dorsal lateral nucleus of the mesencephalon; NCM, caudal medial nidopallium; LLV, ventral

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

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