



Parting self from others: Individual and self-recognition in birds

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ABSTRACT

Individual recognition is the ability to differentiate between conspecifics based on their individual features. It forms the basis of many complex communicative and social behaviours. Here, we review studies investigating individual recognition in the auditory and visual domain in birds. It is well established that auditory signals are used by many birds to discriminate conspecifics. In songbirds, the neuronal structures underpinning auditory recognition are associated with the song system. Individual recognition in the visual domain has mainly been explored in chickens and pigeons, and is less well understood. Currently it is unknown which visual cues birds use to identify conspecifics, and whether they have cortical areas dedicated to processing individual features. Moreover, whether birds can recognise *themselves* visually, as evidenced by mirror self-recognition, remains controversial. In the auditory domain, the responses of neurons in the song system suggest identification of the bird's own song. The surveyed behavioural and neural findings can provide a framework for more controlled investigations of individual recognition in birds and other species.

1. Introduction

Individual recognition is broadly defined as the ability to discriminate different conspecifics based on their individual features (Dale et al., 2001; Tibbetts and Dale, 2007) and across different situations (e.g., Bee and Gerhardt, 2002). It is thought to be a corner stone of communication and cooperation, and can be beneficial for complex social behaviour such as dominance hierarchy or parental care (Mateo, 2004; Tibbetts and Dale, 2007). For example, pinyon jays (*Gymnorhinus cyanocephalus*) can infer their own hierarchical status relative to a stranger from observing its interactions with familiar individuals (Pazy-Miño et al., 2004): here, recognising individuals allows the jays to avoid potential costly interactions with a unknown but dominant conspecific. Another example is the breeding behaviour of the emperor penguin (*Aptenodytes forsteri*). Emperor penguins do not have a nest, and thus mated partners cannot use topographical cues to find each other – rather they recognise each other's calls. To do so, they use two-voice system that allows them to convey identity information over distance and through obstacles (Aubin et al., 2000). Thus, parental care in emperor penguins relies on mutual recognition of the parents.

Mate recognition, as in the example above, is often inferred when a special treatment of one individual compared to all other individuals is observed. However, such a behavioural pattern not necessarily reflects *true* individual recognition. It has been argued that such mate recognition might in fact reflect *class* recognition – the ability to

distinguish between the class 'mate' and the class 'non-mate' (Thom and Hurst, 2004). According to this argument, true individual recognition can only be inferred when a differential response between more than one individual can be observed. Consequently, it is debated whether recognising the voice of a mate or a kin, for instance, constitutes 'true' individual recognition (Tibbetts et al., 2008).

As advantageous as recognising individual conspecifics may seem *prima facie*, it comes at a price in the form of cognitive demand (Yorzinski, 2017). An animal has to first perceive and attend to the characterising features of different individual conspecifics that are very similar in appearance. The animal then has to associate and memorise these features to recognise the individual at a later point in time (Leopold and Rhodes, 2010). In addition, these features need to be generalised to many different environmental conditions. Such memory processes constitute a fitness cost (Burns et al., 2010; Mery and Kawecki, 2003) and may increase predation risk (Dukas, 1999). Overall, however, individual recognition is expected to be of adaptive value due to a prevalence of benefits and therefore to be subject to selection pressures (Wiley, 2013).

The need for individual recognition is expected to be reflected in specialisations of the brain. In primates, for instance, which interact and cooperate frequently with multiple different individuals on whom they depend (Adolphs, 2003; Tomasello, 2014), sociality dictates rapid assessment of individuals. It has been suggested that nonhuman and human primates have evolved dedicated neuronal structures that

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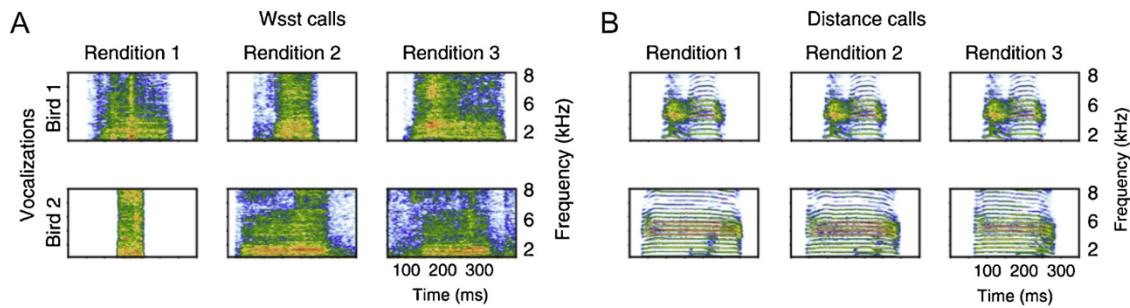


Fig. 1. Acoustic variability in zebra finch calls. Three renditions of 'Wsst' calls (A) and of distance calls (B) of two zebra finch males (adapted with permission from Elie and Theunissen, 2018).

allow them to do so (Tibbetts and Dale, 2007) – for example, the face-system in the temporal lobe of monkeys (Tsao et al., 2006) and the fusiform face area that is especially responsive to faces in humans (Kanwisher and Yovel, 2006). At least in primates, the importance of recognising others is manifested in the brain.

Individual recognition is ubiquitous in the animal kingdom and found in many animal taxa – from different vertebrates to arthropods (e.g., D'Etorre and Heinze, 2005; Falls, 1982; Höjesjö et al., 1998; Myrberg and Riggio, 1985; Proops et al., 2009; Snowdon and Cleveland, 1980; Tibbetts and Dale, 2007; Wiley, 2013). In this review we focus on birds. Birds have received substantial attention in neuroethology due to the rich behavioural repertoire and impressive cognitive capabilities of some avian representatives, such as corvids (Ditz and Nieder, 2016; Emery and Clayton, 2004; Nieder, 2017; Smirnova et al., 2015). We address the questions which sensory features are exploited when birds recognise each other, and what neuronal mechanisms are at work to support this capability. Along this line, we explore the putative behavioural signatures and neural substrates of individual recognition in birds.

2. Examples of individual recognition in birds

Many reports showcase impressive individual recognition in birds. Tinbergen, 1953 for example recounts the herring gull's ability to make out its mate among a large congregation of conspecifics (Tinbergen, 1953). Additionally, more indirect examples can be found in studies investigating social cognitive abilities. In order to display these abilities, birds need to recognise individuals. For instance, California scrub-jays (*Aphelocoma californica*) are known to protect their cached food items from pilfering conspecifics (Dally et al., 2006a). In one study, scrub-jays were successively observed by two conspecifics A and B while they were caching. When being observed by conspecific A, they could only cache in tray 1, while a second tray 2 was present but made inaccessible. The opposite was the case when they were observed by conspecific B. Later, when they had the chance to recover food items to safety in the presence of either one of the competitors, say conspecific A, they were more likely to recover and remove food previously cached in the presence of conspecific A, disregarding caches made in the presence of conspecific B. It seems that the scrub jays perceived observer A as threat only to the caches it knew about – that is, the one that had been cached in the presence of conspecific A (Dally et al., 2006b). This study shows that scrub-jays can differentiate between conspecifics A and B. The scrub-jays behaved differently when confronted with two different individuals, both of which were known to them and were not of two inherent classes (such as, male-female, known-unknown, or kin-non-kin).

The importance of individual recognition is also evident in less competitive contexts: ravens (*Corvus corax*) adjust their willingness to cooperate with a partner based on individual identity (Massen et al., 2015). Here, the ravens seem to take into account the outcome of previous cooperative interactions with different individuals. They

cooperated less in a later trials with individuals that monopolised the food reward in the first encounter. Hence, ravens differentiate between conspecifics, and likely associate the outcome of an interaction with individual conspecifics.

3. Different sensory modalities of individual recognition

What cues do birds use to recognise conspecifics? A range of potential cues from different sensory modalities is available. Because birds typically rely on auditory and visual stimuli, we here focus on visual and auditory as well as cross-modal recognition.

3.1. Auditory recognition

3.1.1. Behavioural studies

Individual recognition based on auditory cues is crucially important for birds in many different contexts. For example, ravens seem to remember the nature of their relationship with group members that they can recognise based on vocalisations alone (Boeckle and Bugnyar, 2012). Consequently, individual voice recognition has received a lot of attention in birds (see for example Brooks and Falls, 1975; Weary and Krebs, 1992).

To allow individual recognition, differences within an individual's vocalisations need to be less pronounced than differences between individuals. Inter-individual variety of voice characteristics has been reported for songbird species such as the pied babbler (*Turdoides bicolor*; Humphries et al., 2016), rooks (*Corvus frugilegus*; Benti et al., 2019), zebra finches (*Taeniopygia guttata*; Elie and Theunissen, 2018; see Fig. 1) or the screaming piha (*Lipaugus vociferans*; Fitzsimmons et al., 2008). Because corvids can intentionally produce vocalisations (Brecht et al., 2019), one might expect that some songbirds can also cognitively control the acoustic features of their vocal output in the service of individual recognition. Inter-individual variability of vocalisations has also been described for birds outside the passerine order, such as the greater prairie-chicken (*Tympanuchus cupido*; Hale et al., 2014), peahens (Yorzinski, 2014) or budgerigars (*Melopsittacus undulatus*; Dooling et al., 1992). Of course, vocalisations are always at risk of being affected by environmental factors affecting acoustics (Forrest, 1994; Patricelli and Blickley, 2006), or the sender's emotional state (Soula et al., 2019). However, it seems that these noise sources may not have detrimental effects. In zebra finches, at least, individual differences are resistant to propagation over distance (Mouterde et al., 2014). Thus, vocalisation differences between individuals seem to outweigh variations occurring within an individual.

Importantly, such vocal differences are not only produced, but can also be perceived: in an operant go/no-go task, jungle crows (*Corvus macrorhynchos*) learned to distinguish contact calls from different individuals and to transfer this to novel calls (Kondo et al., 2010). Similarly, budgerigars can be trained to discriminate contact calls of their conspecifics, but also of their heterospecifics, that is, canaries (Park and Dooling, 1985). This result indicates that the acute hearing system of

birds is sensitive to subtle acoustic differences necessary to distinguish individuals.

Not surprisingly then, the recognition of mates or kin using auditory information derived from innate calls is well established in birds (Dhondt and Lambrechts, 1992). American goldfinch (*Spinus tristis*) females, for example, will respond to the playback of the flight call of their mate, but not to that of a control male (Mundinger, 1970). Roskaft and Espmark (1984) found that rook nestlings respond with less aggression towards a playback of the calls of a sibling, compared to those of an unrelated conspecific, even after 10 months of separation. Pinyon jays showed increased begging behaviour when presented with calls of related adults (McArthur, 1986), and recognition of the approach calls of their mates (Marzluff, 1988). One recent laboratory study trained zebra finches (*Taeniopygia guttata*) on operant condition task where the finches learned the reward value of calls from different individuals. The finches were not only able to generalise across different renditions of the call, but also across different call types from one caller. This finding shows that zebra finches can differentiate between individuals regardless of which call types they heard, such as alarm or contact calls (Elie and Theunissen, 2018). As an exception from this rule, zebra finch parents seem to fail to recognise the distance calls of their offspring among that of other, unrelated juveniles (Reers et al., 2011). Overall, however, mate and kin recognition by acoustic signals is well established in birds.

Songbirds can also recognise the songs of their species (e.g., Goldman, 1973), kin (e.g., Miller, 1979), mate (Blumenrath et al., 2007), or neighbours (e.g., Stoddard et al., 1991). For example, song and white-throated sparrows approach a loudspeaker playing the song of a neighbour at the regular territorial boundary with this neighbour less than when the song is played from the opposite boundary (Falls and Brooks, 1975; Stoddard et al., 1991). This finding suggests that the sparrows associate the song of individual neighbour with a specific location, and not only differentiate between neighbours and strangers.

Note that it is generally assumed that songbirds with a larger song repertoire show poorer individual song recognition because they face increased memory load together with a decrease in relative exposure to each song type (Falls, 1982). For example, due to their song plasticity and flexible use, it has been proven difficult for a classifier to identify Chiffchaffs (*Phylloscopus collybita*) based on their song across longer time spans (Průchová et al., 2017). Thus, research on individual voice recognition usually focusses on songbirds with short and relatively simple songs (Fox, 2008).

Taken together, many bird species are able to differentiate between individuals based on the acoustic features, both of their calls and of their song. It should be noted, however, that not all such reports necessarily imply true individual recognition. Behaviour suggesting individual neighbour recognition could rather demonstrate an ability to associate specific calls or songs with a specific location. Similarly, in the context of kin recognition, for example, it is important to explore whether the bird species in question can differentiate between kin A and kin B, or whether they simply differentiate between their offspring and all other conspecifics.

There is less research on auditory recognition in birds outside the songbird suborder. Budgerigars, a parrot species, are more likely to respond to their mate's call compared to that of other conspecifics (Ali et al., 1993), and peahens of the Galliformes order differentiate between the antipredator calls of different individuals (Nichols and Yorzinski, 2016). By contrast, male greater prairie-chicken (*Tympanuchus cupido*) do not distinguish between the calls from different individuals, although their vocalisations vary between individuals (Hale et al., 2014). The reasons of order-specific differences in auditory recognition await further exploration.

3.1.2. Neuronal basis of auditory recognition

The neuronal structures underpinning auditory recognition are well established in songbird species (see Fig. 2). The first auditory projection

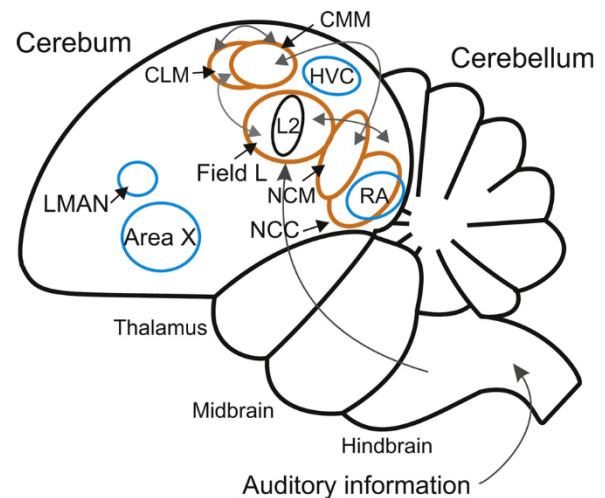


Fig. 2. Schematic representation of the songbird brain and the approximate position of the classic song nuclei (blue) and the brain regions involved in auditory perception (orange). LMAN = lateral magnocellular nucleus of the nidopallium; CLM = caudolateral mesopallium; CMM = caudomedial mesopallium; NCC = caudocentral nidopallium; HVC = proper name; NCM = caudomedial nidopallium; RA = robust nucleus of the arcopallium. Adapted from Berwick et al. (2012) with permission.

zone in the avian endbrain is field L. However, neurons in field L do not discriminate between conspecific song, tutor song and the birds own song (BOS; Meliza and Margoliash, 2012 but see Hauber et al., 2013); this distinction only emerges later in the auditory pathway, in the caudomedial nidopallium (NCM). For example, lesions to the caudomedial nidopallium (NCM), a secondary auditory forebrain region, lead to a decrease in tutor song preference over novel songs, which suggests that the tutor song is represented in NCM. At the same time, NCM lesions do not affect the ability to discriminate sound and, interestingly, female from male calls (Gobes and Bolhuis, 2007), suggesting that there is a dissociation between the neural substrates for auditory recognition more generally and for recognition of the tutors song specifically. Additionally, single cell recordings from NCM show that familiar conspecific songs elicit weaker neural responses compared to unfamiliar songs, thus reflecting associative learning processes involved in song recognition (Thompson and Gentner, 2010).

The NCM is directly connected to the caudal medial mesopallium (CMM), another secondary auditory forebrain region. Neurons in CMM respond selectively to conspecific song compared to other complex stimuli (e.g. Chew et al., 1996; Theunissen et al., 2004). Lesions to the CMM of zebra finches decreased their preference for conspecific as opposed to heterospecific songs (Gobes and Bolhuis, 2007). Additionally, an immediate-early-gene expression study shows that both NCM and CMM are engaged in song recognition tasks for recognition of familiar songs as well as learning of new differentiations in European starlings (Gentner et al., 2004). Another candidate structure is HVC that receives input from the auditory system but also exhibits premotor properties. HVC is considered the dominant sensorimotor hub in the song system. Lesions in HVC in starlings trained to recognise individual songs suggests that HVC plays a role not in the discrimination of individual songs, but rather in the formation of associations between a song and some referent (Gentner et al., 2000). Song recognition requires both the discrimination of acoustic features as well as an association of those features with particular singers, and HVC seems to be important for the latter process.

A special category of song are those that male songbirds sing when addressing females. Such female-directed songs seem to be represented in a specific endbrain region, the NCC (caudocentral nidopallium) of the left hemisphere. Using functional magnetic resonance imaging (fMRI) on anaesthetised females presented with different categories of

songs, the NCC showed selective increase in blood flow to female-directed song (Van Ruijssevelt et al., 2018). In addition, immediate-early gene expressions explored in the same study supported higher neuronal activity during the playback of female-directed song in the NCC. Hence, the NCM, CMM, NCC, and HVC each seem to be involved in different aspects of song recognition and association, which makes them possible candidates for individual song recognition as well.

3.2. Visual recognition

3.2.1. Behavioural studies

Birds are very visual animals (e.g., Clark and Colombo, 2020; Thorpe, 1968). Surprisingly, however, there have been notably fewer attempts to explore avian recognition abilities in the visual domain. The few existing studies primarily investigated species from orders other than Passeriformes, such as species of the Galliformes (chickens) (D'Eath and Stone, 1999; Guhl and Ortman, 1953; Ryan and Lea, 1994), and the Columbiformes (pigeons) (Jitsumori et al., 1999; Shimizu, 1998). Hens, for example, discriminate between familiar and unfamiliar conspecifics using visual cues: they tend to feed more closely to a flock mate when seeing them under white light as opposed to red or blue light (D'Eath and Stone, 1999). Therefore, lighting-dependent visual cues are important for the recognition of conspecifics in chicken.

In songbirds, individual recognition based on visual cues is less well explored. Rooks (*Corvus frugilegus*), for example, have been found to spontaneously look more often at a video of their partner compared that of an unpaired conspecifics (Bird and Emery, 2008). Hence, they can differentiate their partner by visual cues alone as acoustic cues were not available in these videos. It is not clear, however, which feature of the presentation of the partner allowed them to do so (Brecht et al., 2018). Because the preference to look at the partner was not found when the stimuli were presented as static pictures, it is possible that the differentiation was based on the recognition of individual-specific movement patterns or behaviour of the partner present in movies, rather than static visual features, such as the 'face', in a picture.

Which visual cues then are important for individual recognition in the visual domain? A number of features could be relevant, such as 'face' and gait, but also body shape or plumage coloration. Budgerigars can learn to recognise a conspecific from pictures alone, predominantly using individual characteristics of the head area (Brown and Dooling, 1992; Trillmich, 1976). In a matching-to-sample task, carrion crows (*Corvus corone*) learned to recognise pictures of the 'facial' profile of crows (Fig. 3) (Brecht et al., 2017). The importance of the head area has also been found in birds spontaneous behaviour: pigeons (*Columba livia*)

show more courtship behaviour to a video of a female pigeon's 'face' as opposed to its body (Shimizu, 1998), and can learn to discriminate the pictures of conspecifics' faces (Watanabe and Ito, 1990). However, there is also evidence that the configuration of the features is less important for birds than for mammals: in contrast to humans (Carey and Diamond, 1977; Diamond and Carey, 1986), sheep (*Ovis aries*) (Kendrick et al., 1996) and chimpanzees (*Pan troglodytes*; Dahl et al., 2013), carrion crows do not show a face inversion effect, that is, they recognise upright and inverted faces just as easily. This result indicates that they do not seem to process conspecifics' profile faces in a specialised, holistic manner (Brecht et al., 2017); (see Fig. 3C). Similarly, male pigeons did not discriminate between intact normal faces and faces in which local features were spatially rearranged (Patton et al., 2010). However, chicks that have no visual experience with faces tend to preferably approach stimuli with a triangular face-like arrangement, as opposed to nonface-like schematic stimuli (Rosa-Salva et al., 2010). This finding supports the presence of a potentially innate face-specific mechanism in chicks, and maybe in birds in general. The apparent discrepancy between the apparent relevance of 'facial' configuration in precocial chicken and the altricial pigeons and crows might be related to a difference in ecology and development, which might in turn manifest itself in a different way to process social stimuli (Ryan and Lea, 1994).

Certain features of the face might also be more important than others. In pigeons, altering or removing the beak has a greater influence on mate choice, compared to a manipulation of the eyes (Patton et al., 2010). Similarly, Kondo and Izawa (2014) showed that the shape of the jungle crows beak is sufficiently diverse to allow a classifier to identify individual crows. Whether the crows actually use this feature is unknown.

Ultraviolet light reflecting plumage is common in birds (Eaton and Lanyon, 2003), and might provide another source of visual recognition. It has been proposed that for certain bird species, the ultra violet coloration of the plumage might be relevant, for example when choosing a mate (Rajchard, 2009) but also in agonistic relationships (Poesel et al., 2007). Most bird species also have four cone types (Smith et al., 2002), suggesting tetrachromatic vision including ultraviolet vision (Burkhardt, 1996; Finger and Burkhardt, 1994). This is true for many passerine songbird species, such as zebra finch (Bowmaker et al., 1997), starling (*Sturnus vulgaris*, Smith et al., 2002) and Pekin robin (*Leiothrix lutea*, Maier and Bowmaker, 1993), as well as for parrots (Odeen and Hastad, 2003). However, not all bird species are sensitive to ultraviolet light: the visual system of birds of the Corvidae and Tyrannidae family as well as raptor species is biased towards violet light (Odeen and Hastad, 2003). Consequently, although UV coloration is an important

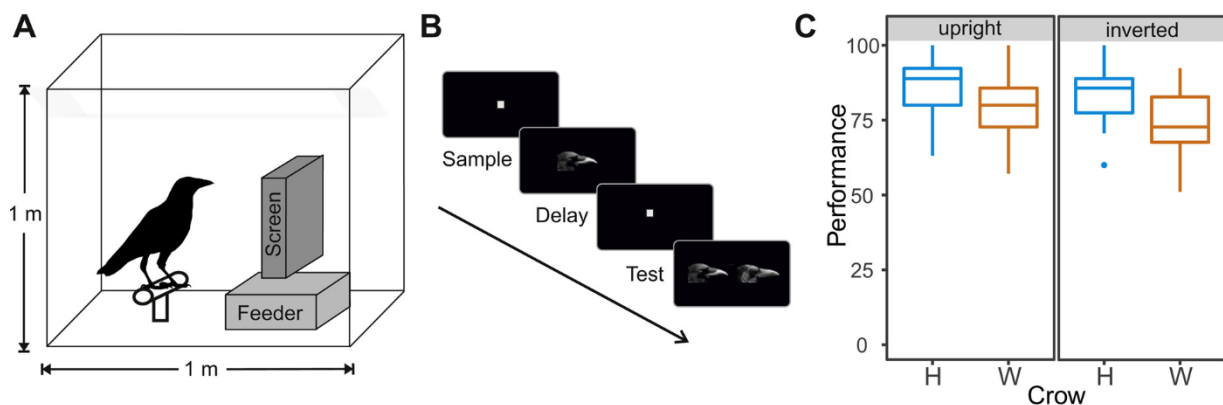


Fig. 3. Face-inversion in the carrion crow. Schematic of the setup used to test the crows (A). Match-to-sample task presented on a touch screen, where the crows had to peck the test stimulus that matched the sample (B). Box-and-whiskers plot showing the performance of two crows (crow H = blue, crow W = orange) in the match-to-sample task when discriminating crow profiles (C). The boxes signify the upper and lower quartiles; the median is represented by the horizontal line. The whiskers extend from the box to values no further than $\pm 1.5 \times \text{IQR}$ from the box. The dot signifies an outlier. Performance was well above chance for the two crows, both when the pictures were presented upright (left panel) and inverted (orange panel). The crows did not show a face inversion effect as performance was not influenced by the orientation of the pictures presented. Taken with permission from Brecht et al. (2017).

signal, it is less clear whether UV-differences in plumage are used to recognise individuals, and if so, how widespread this feature is.

3.2.2. Neuronal basis of visual recognition

Tasks involving recognition of faces and other familiar stimuli activate a system of face-selective areas ('patches') in the temporal lobe of nonhuman primates and sheep (Bruce et al., 1981; Kendrick and Baldwin, 1987; Tsao et al., 2006). In these temporal lobe regions, almost all of the visually responsive neurons are strongly face selective, meaning that they do not respond to any complex visual stimulus but faces specifically. This neuronal selectivity indicates that a dedicated cortical area exists to support face processing in primates. Similarly, the so-called fusiform face area located in the fusiform gyrus at the occipito-temporal border is a key area for the representation of face identity in humans (for a review see Kanwisher and Yovel, 2006). It was therefore hypothesised that also the avian brain could exhibit such a dedicated facial representation. However, evidence for this prediction is currently lacking.

A study in American crows used positron emission tomography (PET) and explored cerebral blood flow as an indirect brain signal to explore neural correlates of face representation. In this study, wild crows were familiarised with 'threatening' (associated with threatening situations) and 'caring' (associated with caring situations) human face masks. Prior to PET measurements, crows were injected with radioactively labelled glucose (that is known to accumulate in the brain in proportion to regional brain activity) and were shown either 'threatening', 'caring' or no masks. After this glucose uptake period, the crows were anaesthetised and imaged. A contrast of the obtained regional activity patterns in the different groups of crows suggested that, at least for human faces, the rostral nidopallium might be important (Marzluff et al., 2012). However, it should be noted that the face masks might not have been categorised as human faces by the crows. Because non-face controls were missing, the reported activation pattern could simply reflect a general brain signal related to any salient stimulus that the crows previously had associated with positive or negative consequences.

Direct electrophysiological recordings of the neuronal activity of single neurons could not confirm face selectivity in the avian brain. A single-neuron recording study in pigeons failed to find face-selective neurons in different higher-order endbrain regions (Clark et al., 2019). Single-unit activity was measured in pigeons while they performed a task that required them to discriminate between two sets of stimuli that included images of pigeon faces. Recordings were sampled from four visual forebrain structures of the tectofugal visual pathway: the entopallium, mesopallium ventrolaterale, nidopallium frontolaterale, and area temporo-parieto-occipitalis. No neurons fired selectively to only faces in either of these areas (Clark et al., 2019). In addition, Scarf et al. (Scarf et al., 2016) report a lack of conspecific-specific neuronal response in pigeon nidopallium, hippocampus, entopallium and arcopallium. Similarly, face-selectivity was also absent in neurons of the nidopallium caudolaterale (NCL) of crows performing a delayed matching-to-sample task with human faces and bird heads as sample stimuli (Veit et al., 2014). The absence of face-selective neurons suggests that the birds' solution to the challenges of individual recognition may be mechanistically different to mammalian species, but can also be explained by divergences in birds' visual physiology and behaviour in visual discrimination tasks (Clark et al., 2019).

Previous behavioural research has also investigated the possible lateralisation of brain hemispheres in social recognition. In chicks as well as in quails, the right eye (suggesting left hemispherical control) is used when a novel stimulus is presented, social or asocial. After familiarisation, the birds switch to the left eye (suggesting right hemispheric control), which was then also used to discriminate between conspecifics (Vallortigara and Andrew, 1994, 1991). Studies on an altricial songbird species, the Australian magpie (*Gymnorhina tibicen*), has found that the magpies lateralised eye use was similar to that of chicks

(Koboroff et al., 2008). This opens the possibility that the results from precocial species, such as chicks, could possibly be generalised to other bird species.

3.3. Cross-modal recognition

3.3.1. Behavioural studies

In many situations, animals have more than one modality at their disposal; visual cues are often supplemented by auditory or olfactory cues, which may allow a recognition transfer across modalities. In addition, using stimuli from different modalities provides a good test for 'true' individual recognition (Yorzinski, 2017). For instance, the 'violation-of-expectation' protocol allows to test directly for individual recognition as opposed to class recognition. In such tests, animals are first confronted with a signal from an individual in one modality, and then confronted with a signal from either the same (congruent situation) or a different individual (incongruent situation) in the other modality. The hypothesis is that the subjects expect that both cues refer to the same individual (congruent); if this expectation of the subjects is violated, the subjects are expected to be surprised and therefore to look longer at the incongruent outcome.

Currently, the only study of cross-modal recognition in birds comes from jungle crows (Kondo et al., 2012). In this study, jungle crows were presented with visual and auditory cues of conspecifics from group members as well as outsiders. The crows could first see a conspecific (e.g., individual A), and then, out of view, hear a contact call. The call was either matched (congruent) to the individual that was just visible (e.g., contact call from individual A), or not matched (incongruent) (e.g., contact call from individual B). Only a small opening allowed the crows to inspect the adjacent cage where the conspecific was kept. When the identity of the caller and of the individual just visible did not match, the crows were faster to approach the opening and looked longer. Importantly, this pattern was not found when the stimulus bird was unfamiliar to them. This finding has been interpreted as the test subject expecting to hear the contact call of individual A following the sight of individual A, and not the contact call of individual B. This violation of expectation caused them to look longer (Kondo et al., 2012). This result represents evidence that jungle crows can recognise individuals from their group and is an example of true individual recognition in birds.

3.3.2. Neuronal basis of cross-modal recognition

The putative neuronal correlates of cross-modal individual recognition are even less explored than unimodal recognition phenomena. One high-level avian endbrain area that is known to be involved in association learning is the nidopallium caudolaterale (NCL), which would be a good candidate for learned cross-modal individual recognition. Neurons in the crow NCL can be trained to associate arbitrary stimuli (Veit et al., 2017), and have also been shown to associate stimuli from different (visual and auditory) modalities across temporal gaps (Moll and Nieder, 2015). If the NCL encodes not only inanimate stimulus associations, but also animate agent associations, this brain area could also play an important role in this type of social cognition.

4. Recognition of self

Birds can recognise their conspecifics. However, can they also recognise themselves? One early example of visual self-recognition outside the primate lineage comes from a bird species, the magpie (*Pica pica*; Prior et al., 2008). We here review the current status of visual and auditory self-recognition in birds.

4.1. Visual self-recognition

Most famously, self-recognition has been tested with the Mirror Mark test, developed by Gallup (Gallup, 1969). Animals are marked

with paint or a self-adhesive sticker in a place on their body that is hard or impossible to see. Animals are then presented with a mirror. If they recognise themselves in the mirror, they should then try to reach and remove the sticker or paint mark ('mark-directed behaviour'). Sham markings as well as no-mirror controls (i.e., the animal is marked, but has no mirror to inspect the mark) are introduced to rule out explanations related to tactical cues or handling during the marking. Aside from species of great apes and a few mammalian species, magpies and Indian house crows (*Corvus splendens*) are the only avian species that spontaneously showed increased mark-directed behaviour when presented with a mirror, as opposed to when no mirror is present (Buniyaadi et al., 2019; Prior et al., 2008). Interestingly other corvid species such as jackdaws (*Corvus monedula*; Soler et al., 2014) and carrion crows (Brecht et al., 2020; Vanhooland et al., 2019) failed the mirror mark test. For other corvid species, the results are mixed. Clary and Kelly (2016) presented Clark's nutcrackers (*Nucifraga columbiana*) with a modified mirror mark test: the birds were confronted with blurred (providing only motion contingency information) as well as clear mirrors (providing identity and motion contingency information). Here, some individuals showed an increase of mark-directed behaviours in the blurred mirror condition. The authors argue that a blurred mirror might reflect the nutcrackers natural experience, as opposed to a 'perfect' mirror, as in nature, reflections are often distorted. A blurred mirror filters identity information, and might give the birds the possibility to attend to their motion information (Clary and Kelly, 2016). However, it should be noted that there is no need to use a 'blurred' mirror with great apes who have arguably also no 'perfect' mirrors in their natural environment.

The applicability of the mirror-mark test on non-primate animals has been debated (De Veer and van den Bos, 1999). Other protocols have thus been developed. The motivation of corvids to protect their cached food items from conspecifics has been utilised to this end, asking whether they would protect their caches from their own mirror image. Clark's nutcrackers could cache either alone, with a conspecific present or in front of a mirror (blurred and not-blurred). The nutcrackers suppressed caching when they were observed by a conspecific or confronted with a clear mirror reflection of themselves. In the blurred mirror condition, however, they cached as if they were alone, suggesting that they understand that their blurred mirror image is no treat to them (Clary and Kelly, 2016). The use of caching to test mirror recognition has also been employed in California scrub-jays (Clary et al., 2020; Dally et al., 2010). In both studies, when confronted with a (clear mirror), scrub-jays cached as if they were alone, suggesting that they do not see the mirror as a conspecific. Whether they understand the mirror image as themselves, or a non-threatening (e.g., subordinate or familiar) conspecific is however still unclear as previous studies have shown that jays attend to the behaviour of an observing conspecific (Ostojić et al., 2017). Consequently, the lack of cache protection in front of a mirror could be explained more parsimoniously: The birds might have perceived their mirror image as an unthreatening conspecific that was concerned with its own caches. In line with this suggestion, jungle crows respond to their mirror image with aggression, suggesting they perceive it as a conspecific, rather than a mirror reflection (Kusayama et al., 2000).

In non-corvid bird species, the results are negative. An extensive investigation of great tit (*Parus major*) mirror recognition has found no individuals passing the mirror mark test (Kraft et al., 2017). In addition, neither keas (*Nestor notabilis*) nor Goffin's cockatoos (*Cacatua goffiniana*) have passed the mirror mark test (van Buuren et al., 2018). Similarly, lesser flamingos (*Phoeniconais minor*) respond with marching displays when presented with a mirror (Pickering and Duverge, 1992), suggesting that they treat it as a conspecific, and do not understand their mirror reflection. Note, however, that pigeons can be trained to pay attention to their mirror image (Epstein et al., 1981; Uchino and Watanabe, 2014). Thus, the issue of mirror self-recognition in birds remains controversial.

4.2. Auditory self-recognition

Because avian vocalisations, especially those of songbirds, are very well studied, we know much more about how birds respond to their own vocalisations, known as the bird's own song (BOS). It has been proposed that the BOS represents an autogenous reference when listening to conspecific songs (Hinde, 1958; Margoliash, 1986), thereby aiding song learning. Thus, the BOS is particularly relevant because as true vocal learners, songbirds have to learn their song from a conspecific tutor, usually the father.

Because of its importance for songbirds, it has been a longstanding question whether the BOS is perceived as 'self' (Derégnaucourt and Bovet, 2016). This question is usually studied by playing this song back to the focal individual. In such a study, song sparrows were confronted with their BOS, as well as songs with different degrees of similarity while their territorial response to the different songs was measured. The strength of the territorial response increased with the dissimilarity of the song to the BOS (McArthur, 1986). This finding suggests that the BOS is perceived as separate from the songs of conspecifics, and has been interpreted as indicating an auditory concept of 'self' (but see Suarez and Gallup, 1987). However, songbirds responses to their own song vary greatly between studies and species and remain inconclusive: some studies report a strong territorial response (Searcy et al., 1981), others none at all (Searcy et al., 1981; Stoddard et al., 1992). Thus, the predictions about how a songbird would react to hearing its own song are not straightforward; the focal individual could be agitated, habituated or indifferent to hearing its own song. In addition, a discriminatory response of the subject to a presentation of its BOS, compared to other conspecifics song, need not imply a perception of this song as 'self' but rather could reflect surprise or irritation about the distortion of the song when heard from a tape (Derégnaucourt and Bovet, 2016).

Neural representations of acoustic self-recognition have been explored in the song brain nuclei of the songbird song system. One of the prime candidates early on was song nucleus HVC that operates at the apex of a sensorimotor hierarchy for song (Nieder and Mooney, 2019). HVC neurons encode both the motor production of song elements (Long and Fee, 2008; McCasland, 1987), but respond also when the awake songbird hears song (Dave et al., 1998; George et al., 2005; Margoliash, 1986; McCasland and Konishi, 1981) and thus help to determine the perception of species-specific song (Brenowitz, 1991). HVC thus serves premotor as well as auditory function. Interestingly, the auditory responses can be quite specific, and certain HVC neurons in awake songbirds respond primarily to playback presentations of the BOS (McCasland and Konishi, 1981; see also Fig. 4). Of course, responses to BOS are confounded by a much higher familiarity and its importance during song learning. Still, the responses of BOS-sensitive neurons could constitute a neuronal signature of the bird (implicitly) recognising its own song, thereby acoustically differentiating itself from others.

Remarkably, some of these neurons also switch between perceptive (hearing) and expressive (singing) representations of the BOS. Recordings in freely behaving songbirds showed that a subset of a specific class of HVC neurons (those projecting to song nucleus Area X) are similarly active both during singing and BOS playback (Fujimoto et al., 2011; Prather et al., 2008). Such neurons elicit neuronal impulses at exactly the same time during the song, irrespective of whether the recorded bird is singing itself or listening to its song playback. Control experiments showed that these responses cannot be explained by auditory feedback from the bird during singing. Rather, the neurons switch from encoding auditory aspects of the BOS to purely motor-related activity as the bird shifts from listening to its own song to singing it. In other words, they mirror perception and production of the BOS. These auditory-vocal 'mirror neurons' in HVC are likely to contribute to song and therefore individual recognition; they are ideal candidates for enabling song recognition in the realm of the individual's own song repertoire (Mooney, 2014).

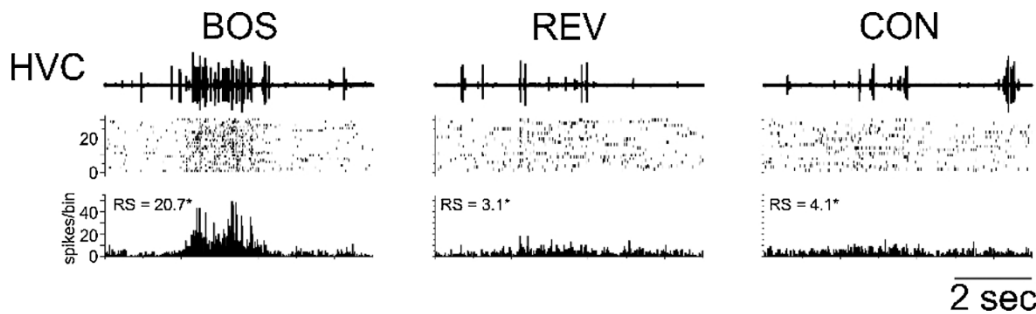


Fig. 4. Extracellular electrophysiological recordings from anaesthetised zebra finches' HVC in response to a playback of the bird's own song (BOS), of the BOS in reverse (REV), and of a con-specific song (CON). Upper row shows raw data for a single playback of each song, middle row shows a raster plot of activity of thirty iterations of each song, and lower row shows the peristimulus time histogram (PSTH) of the cumulative response of each song (taken with permission from Williams et al., 2012).

5. Conclusion

Recognising conspecifics on an individual basis comes with cognitive costs, but also has many advantages. Here, we reviewed studies investigating individual recognition in birds in the auditory and visual domain. It is well established that birds can recognise individual based on their voice, for example in that they differentiate the song from their neighbour on their territory boarder A from neighbour on boarder B. However, not all findings imply true individual recognition but could simply demonstrate an ability to differentiate between auditory signals more generally, such as the ability to notice differences in songs between different boarders. Further studies are therefore necessary to disentangle individual recognition and class recognition (e.g., kin vs non-kin).

In the auditory modality, songs and vocalisations in general are used by birds to discriminate conspecifics in many different contexts, and some species can even exploit acoustic features to derive rank and long-term relationship information. Corvid songbirds, in particular, exploit acoustic features to derive the identity and rank of individuals. Neuronal structures associated with hearing and producing song in songbirds have been associated with auditory individual recognition. The response properties of neurons in the part of the song system responsible for hearing are well suited to discriminate the songs of conspecifics, mates, tutors, and the bird's own song. Selected song nuclei are involved in different aspects of song recognition and association with different behavioural contexts, rendering them possible neuronal candidate structures for individual song recognition.

Individual recognition in the visual domain is less well studied and focusses mainly on chickens and pigeons. This imbalance poses the question whether species that use voice recognition can also recognise each other visually. Penguins for example recognise their mate by voice, but not visually (Jouventin, 1982). In addition, we identify an absence of research asking *which* visual cues are of relevance when differentiating between conspecifics. Furthermore, it remains unclear whether birds have cortical areas dedicated to processing such cues, akin to what has been found in mammals.

As we review above, birds can recognise their conspecifics, but whether they can recognise themselves is less clear. So far, only two bird species of the corvid family, the magpie and the Indian house crow show signs of self-recognition; however, we notice a lack of replications of this initial finding in magpies specifically, and a wealth of ambiguous and sometimes contradictory findings in other corvid species more generally. Auditory self-recognition has been explored in songbird species specifically – in particular, the response to the birds own song, the BOS, and its neuronal correlates.

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Declaration of Competing Interest

None.

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