



# Article Audition and Hemispheric Specialization in Songbirds and New Evidence from Australian Magpies

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**Abstract:** The neural processes of bird song and song development have become a model for research relevant to human acquisition of language, but in fact, very few avian species have been tested for lateralization of the way in which their audio-vocal system is engaged in perception, motor output and cognition. Moreover, the models that have been developed have been premised on birds with strong vocal dimorphism, with a tendency to species with complex social and/or monomorphic song systems. The Australian magpie (*Gymnorhina tibicen*) is an excellent model for the study of communication and vocal plasticity with a sophisticated behavioural repertoire, and some of its expression depends on functional asymmetry. This paper summarizes research on vocal mechanisms and presents field-work results of behavior in the Australian magpie. For the first time, evidence is presented and discussed about lateralized behaviour in one of the foremost songbirds in response to specific and specialized auditory and visual experiences under natural conditions. It presents the first example of auditory lateralization evident in the birds' natural environment by describing an extractive foraging event that has not been described previously in any avian species. It also discusses the first example of auditory behavioral asymmetry in a songbird tested under natural conditions.

**Keywords:** auditory perception; auditory lateralization; song production; extractive foraging; visual laterality; memory; Australian magpie

# 1. Introduction

Field studies of behavioural laterality in birds are still relatively rare, but the few undertaken so far have shown that laterality may play a role in vigilance behaviour [1,2], in predation and sexual behaviour [3,4] and even in tool manufacture, as shown in the New Caledonian crow, *Corvus moneduloides* [5]. In fact, in the special case of tool use and manufacture by crows, the activity appears to be strongly lateralized because birds were seen to use their right eye even when this posed some difficulties [6].

Asymmetries in avian species have been found in visual processing from sensory input to motor output, admittedly largely in domestic chickens [7,8] and pigeons [9]. Lateralized foot use has been shown in pigeons [10,11], the New Zealand kākā [12], some songbirds (sittellas and crested shrike-tits [13]), Japanese jungle crow [14] and also in cockatoos and some parrots [7,15–17]. This paper will explore whether such lateralities, as shown in the visual behavior of many vertebrate species [18], may also be present in auditory abilities and their behavioral expressions in birds.

Without a doubt, vision and audition are the most well-developed sensory abilities both in birds and in humans, and they are often used in conjunction: for example, there is plenty of evidence that learning is particularly effective and often more powerful when vision and audition are coupled [19,20]. In many oscine birds, song learning occurs in a visual context, suggesting that both auditory and

visual perceptual systems could be involved in the acquisition process. Hultsch et al. [21] examined, in male juvenile nightingales, whether song performance improved after coupling visual with auditory stimuli. It did and did so convincingly [21]. In a study on chickens, Van Kampen and Bolhuis [22] demonstrated that learning is improved through compound training with simultaneous exposure to visual and auditory stimuli, showing that either modality has some facilitating effects on the memorization of features from the other modality. Such coupling has also worked in the combination of visual with aversive olfactory stimuli [23]. Additionally, there is evidence from research on zebra finches that visual stimuli activate auditory brain areas, e.g., the HVC, formerly called high vocal centre, now called HVC and used as a proper noun (see Figure 1 below) [24]. Given this interaction between auditory and visual processing and, since visual lateralization is widespread in avian species, it could be that auditory processing is also lateralized.

The importance of asymmetry in song production was identified early by Nottebohm [25]. He found that when the HVC in the left hemisphere was lesioned, male canaries could not produce song. When the HVC in the right hemisphere was lesioned, it had no effect on song production [25]. However, such lateralization does not apply to song production in all species, since it has been shown in zebra finches that some perceived manifestations of lateralization in the HVC during song production proved to be rapid switches between hemispheres and that the overall contributions of both sides were actually equal [26].

In research on memory formation, hemispheric dominance has been found in zebra finch males. Gobes and Bolhuis [27] showed that tutored-song memory and a motor program for the bird's own song have separate neural representations in the songbird brain. Lesions to the caudomedial nidopallium (NCM) of adult male zebra finches impaired tutor-song recognition, but did not affect the males' song production or their ability to discriminate calls. Lesions were bilateral, so any potential lateralization could not be measured. Moorman and colleagues [28] recently measured neuronal activation during sleep in juvenile zebra finch males that were still learning their songs from a tutor. They found that during sleep, there was learning-dependent lateralization of spontaneous neuronal activation in the NCM. Birds that imitated their tutors well were left dominant, whereas poor imitators were right dominant, similar to language proficiency-related lateralization in humans. Indeed, interest in comparative work in song production and perception and human speech [29] has increased substantially in the last decade, finding important similarities in the role of specific auditory nuclei between humans and birds [30,31].

# Limitations: Species Investigated

The species most often chosen for detailed neurobehavioral research on auditory perception/song performance is the zebra finch. The choice makes sense on a number of levels: the song of this species is relatively simple and has a defined learning period, the birds are easy to keep in a laboratory setting (opportunistic breeders as they are, they reproduce easily in captivity and over short periods of time).

However, research of song in zebra finches has some limitations. The zebra finch is a sexually dimorphic bird in which only the male sings. This is not the case in all avian species. In fact, the zebra finch has model character only for songbirds with credentials similar to itself [32,33]; these include, for instance, migratory songbirds of high latitudes that need to fit a complete reproductive time-table into the shortest possible time frame: find a mate in spring, breed, raise offspring and migrate in autumn. Under such circumstances, offspring have to become independent rapidly. Juvenile males have to be taught how to be able to compete and win a female, relying on recall and a perfect memory of the song that an adult male tutor may have taught them in the previous year [34,35].

Having chosen such a model for research on bird song may have implied a questionable underlying assumption that song in all songbirds is purely a male activity (be this for courtship or territorial display) and may be exclusive to the breeding season. The zebra finch model also implies that song is mostly or always crystallized early in development with limited or non-existent ability for any ongoing learning/brain plasticity. However, as has always been known, there is a considerable number of songbirds with vast and flexible repertoires [36], and some of these live in complex social groups. Burish et al. [37] argued that telencephalic volume is strongly correlated with social complexity. This correlation, so they show, accounts for almost half of the observed variation in telencephalic size, more than any other behavioral specialization examined, including the ability to learn song. Moreover, female song is widespread and ancestral in birds [38–41]. In other words, as was recognized some time ago, relying on the zebra finch model in terms of broader questions of behavior could lead to ignoring the importance of social learning in non-reproductive contexts [42,43], the significance of variability in avian communication outside the breeding context and the possibility of different underlying mechanisms of brain activity [44–46] for hearing and vocal production, of which lateralization may be an important manifestation.

Since the discovery of mirror neurons in birds by Prather and colleagues [47], we also know that birds can learn song without being actively supervised and instructed by an adult. Tchernichovski and Wallman [48] explain that, on input, the motor signal is delayed, and this implies that the mirror neurons are providing a 'corollary discharge' signal: that is, a neural representation of the song being heard is available to the bird on first hearing it, and the bird can now check the encoded version against the song it later sings; or expressed differently, the bird has the same neuron activation whether it sings or just listens and gets a copy of the song in its memory against which it can judge its own output (performance) of the song.

Importantly, the mirror neurons identified by Prather et al. [47] belong to a population of neurons that is not replaced, as other neurons in the song system are [49], but is stable across song development. It is this stability that enables the juvenile to improve its song as the memory trace of the correct version remains present and can be accessed. It was established decades ago that amongst the network of nuclei involved in song perception and production, some are essential and some are not essential for song production [50], as discussed below.

# 2. Song Control System, the Auditory System and Lateralization

Song development and song production entail a set of complex interactions between neurological, physiological and behavioral events, and it has taken more than thirty years of research to begin to understand the nature, type and dynamics of these interactions.

Songbirds possess a network of interconnected nuclei in the fore-, mid- and hind-brain used in the perception and production of vocalizations (see Figure 1) [51]. Furthermore, feedback loops are essential for vocal learning, and these are found only in passerines and parrots (and two species of humming birds), cetaceans and humans. In the former group are the HVC, the robust nucleus of the arcopallium (RA) and the tracheosyringeal component of the hypoglossal nucleus (nXIIts), which are necessary for the acquisition and expression of learned song [50], whilst the latter include Area X and the lateral magnocellular nucleus of the anterior nidopallium (LMAN) [52–54]. All of these main nuclei and some important auxiliary nuclei (Figure 1), represented on both sides of the brain, have been tested for lateralized expression. The budgerigar, a psittacine species, capable of vocal learning, but not classed as a songbird, has multiple forebrain areas for vocal production, but some of these, it appears, are not homologous to those of songbirds [55].

A link has been made sometimes between size of song nuclei and song complexity. It is said that song nuclei tend to be larger in those species that have more complex songs, and the HVC is larger in individuals with larger repertoires [56]. However, the relationship between presence and size of nuclei and actual song performance is not always matched. Gahr et al. [57] found that the male and the female of the African duetting bush shrike, *Laniarius funebris*, produce songs of similar complexity, but the HVC is, nevertheless, sexually dimorphic (larger in the male than in the female). The Australian magpie, *Gymnorhina tibicen*, also duets, and these findings are therefore relevant here. Gahr et al. [57] argued that their results show how misleading it can be to assume a causal relation between sex difference in vocal behaviour and in the size of brain areas involved in song production and learning.



**Figure 1.** Song control system and auditory pathways. (**A**) The song control system. (**B**) Auditory pathways; simplified-arrows indicate flow of activations; right lateral view. (**A**) Song output via the main nuclei, the HVC of the nidopallium; RA, robust nucleus of the arcopallium; LMAN, lateral magnocellular nucleus of the anterior nidopallium; Area X of the striatum; DLM, medial subdivision of the dorsolateral nucleus of the anterior thalamus; DM, dorsomedial subdivision of nucleus intercollicularis of the mesencephalon; Uva, nucleus uvaeformis; nXIIts, tracheosyringeal portion of the nidopallium with HVC shelf (lightly shaded); CLM, caudolateral mesopallium; Field L, large area (light grey) subdivided into L1, L2 and L3; NCM, caudomedial nidopallium; RA, robust nucleus of the arcopallium; Ov, nucleus ovoidalis; MLd, nucleus mesencephalicus lateralis, pars dorsalis; LL, lateral lemniscus subdivided into: LLD, dorsal nucleus; LLI, intermediate nucleus; LLV, ventral nucleus; CN, cochlear nucleus; SO, superior olive (adapted from [58]).

However, our own investigations of the song control system in magpies do not confirm those of Gahr and colleagues [57], as is summarized below. Moreover, unlike model species such as zebra finches, *Taeniopygia guttata*, Australian magpies do not use song as part of a reproductive strategy. Both males and females sing [59], and song in both males and females declines, not increases, during the breeding season and does not appear to play any known role in mate choice [60].

Exciting research in recent years has focused on specific areas of the brain and found intensity invariant neurons in Field L, important for distant conspecific recognition (temporal resolution of 30 ms) and noise invariant neurons for individuals at closer distance with a temporal resolution of just 10 ms [61]. While these areas (NCM and CM) were once just considered secondary auditory areas, they have now been recognized as important loci for conspecific song discrimination and individual song recognition and, as such, have behavioural significance [62–67]. Indeed, Woolley and colleagues [68] identified all nine functional areas in the forebrain and midbrain of the zebra finch (four in the midbrain alone), each of which was shown to play a specific role in extracting distinct complex sound features [68]. With the importance of these areas now identified, it should also be possible to ask whether any of these specific sound inputs activate neurons differentially in the left or the right hemisphere.

Indeed, a study by Poirier et al. [69] using functional magnetic resonance imaging (fMRI) discovered that, in zebra finches, the mid-brain shows neural activation in song recognition of both individual (own) and conspecific song, which is a crucial auditory and cognitive ability. These nuclei, called MLd (dorsal part of the lateral nucleus of the mesencephalon), are located in the midbrain, a subcortical region that, not so long ago, had been considered non-plastic and even 'primitive' [69]. They showed that there was a distinct right-side bias in the MLd, confirming a complex topography across the forebrain regions [70]. In other words, in perception of song, as distinct from

song production, robust evidence is now emerging of lateralization of the mechanisms involved. In starling research, behaviourally-relevant song stimuli were used to test whether the NCM might be a site for categorizing complex communication signals, and it was indeed confirmed, largely on the right side of the brain [71,72].

There is no need here to catalogue all the various nuclei with lateralized functions in avian auditory perception and song output; in their review on memory-related brain lateralization [73], Moorman and Nicol (2015) published a very useful table listing nuclei concerned, together with the species and lateralized functions. Suffice it to say that avian species that are lateralized do not necessarily have the same side bias: chaffinches, song sparrows and canaries were found to be left lateralized for control of song, whereas the zebra finch is largely right lateralized [51]. The point is rather that the number of species tested is relatively limited and, except for the starling, they belong to a group of birds that are sexually dimorphic, may be short-lived, limited in repertoire and of varying brain plasticity. Each may have its own specific architecture with respect to how and what is lateralized.

It is a contention of this paper that lateralization may well be different, probably stronger and show more functional separation, the more complex a repertoire is and the greater the ability to learn. It is further a contention that in cases of functional changes of song, one might also expect changes in brain activation and different adaptations, particularly in species that, more like humans, show the same vocal capacities in male and female and are life-long learners. Although this hypothesis cannot be fully tested or confirmed in one paper, it would seem an important and necessary task to establish research on such a species, especially for comparative purposes with human vocal development. Australian magpies satisfy these criteria.

### 3. A Life-Long Learner as a Model Species

This paper reports new data and summarizes previous research obtained both in the laboratory and in the field concerned with auditory and visual hemispheric specialization in the Australian magpie, a species native to Australia. The magpie is one of Australia's foremost songbirds apart from the lyrebird. It is territorial, and residents consist of pairs with long-term bonds, their immediate offspring of one year and sometimes those of previous years.

The main reasons why magpies make a very useful model for perceptual research and memory formation is that in both males and females, song does not crystallize. With a lifespan of 25 or more years, they readily add new elements and sequences to their song, and they are also excellent mimics [74,75]. In these qualities, there are substantial overlaps with parrots and specifically with Australian cockatoos, as well as with ravens and crows. We know that they are amongst the most cognitively complex and long-lived birds (sulphur-crested cockatoos: 100 years; galahs: 80 years) [76]. These attributes are not odd anomalies in avian species, as may once have been believed, but may be significant in that these specific characteristics appeared early in avian evolution.

Some researchers concerned with hemispheric specialization have especially raised the question of evolution [77–79], but so far, little has been made of the geographic origin of modern birds. It has been known since the 1980s, but generally scientifically accepted since 2004, that a number of bird lineages and all modern songbirds in the world today arose in East Gondwana, now Australia [80–82], seemingly the only location where lineages survived the mass extinction events of 65 mya, including galliformes and anseriformes [83], to name a few among the precocial birds, although taxonomists still argue about dates [84], and all (altricial) songbirds. Songbirds radiated out from Gondwana to the rest of the world, a process that took tens of millions of years [85,86]. For reasons of similar climate and vegetation, those species that only went as far as the subtropical and tropical islands to the north of the supercontinent and to the tropical regions of northern hemispheric mainlands (the Indian subcontinent was once part of Gondwana) could presumably keep some of the traits they had acquired in Gondwana. Cockatoos probably arose in the Cretaceous [87,88], i.e., belong to the most ancient lineages of altricial land birds, and their highly lateralized footedness and its connection with complex cognition, a link that has been made only recently [16], gains significance given its very ancient origin.

As to songbirds, Sibley's and Ahlquist's broad taxonomical subdivision into Corvida and Passerida [89], although not necessarily used by taxonomists now, is still very useful to explain certain broad commonalities and traits. Corvida contain overwhelmingly birds with complex cognitive abilities (from problem solving, tool use, to measurably larger brain to body ratios) than the Passerida. Zebra finches (a native Australian species) belong to the Passerida, smaller songbirds that were the ones identified as among the main, probably first, 'escapees' from the Gondwanan continent. Magpies and crows belong to the Corvida, the group consisting of many species, in which we find most extant examples of complex vocal behaviour, learning and problem-solving abilities, qualities that significantly and overwhelmingly are present in species forming long-term bonds and/or engaging in cooperative breeding [76,90]. Most of these lineages, including magpies and lyrebirds [74,91,92], are capable of substantial and accurate mimicry. In summary, brain plasticity, large repertoires and often sophisticated vocal communication may require special architectural features in the brain. One could speculate that avian brains of songbirds of ancient lineages, and even of non-songbirds as cockatoos, might also be highly lateralized and be so for other functions [68].

### 3.1. Song Production in Australian Magpies

Magpies have an extraordinarily large repertoire. Strangely, 'repertoire size' in the literature, with a few exceptions [65], tends to mean the number of syllables in a song or total number of identifiably different songs a bird might sing, and is measured as such rather than as the sum total of vocalizations, not only song. To establish the true range of brain asymmetry or the lack thereof, it would seem important to consider the entire range of a bird's utterances (see Figure 2), since these are likely to represent different contexts and functions and may be under different neural control. In addition, there is the question of where and how the brain gets engaged when vocalizations are a matter of affect or are learned and/or intentional, such as in referential signalling [93]. To my knowledge, there is little to no research that has been done on any of these aspects, including any lateralization of their perception or production.

My own fieldwork on magpie vocal behavior identified as many as 27 different alarm calls [94], falling roughly into six distinct types, recognizable in sonograms as highly specific in profile. Field studies playing back alarm calls established that at least one of these calls is a referential alarm call, signalling the presence of an eagle [95]. We then also established the stability of such referentiality in different magpie subspecies and very different locations [96].

It would seem important to learn whether several categories of vocalizations have greater left or right hemisphere activation and what this might tell us. We already know from studies of song learning in zebra finches that new songs learned are memorized in the right hemisphere while the original song (long-term memory) is retrieved from and shows neural activity in the left hemisphere [27]. However, according to the results reported by Olsen et al. [97], direction and strength of laterality depend on how well each song is learned and by whom: The greater the retention of song from their first tutor, the more right-dominant the birds were when exposed to that song; but the more birds learned from their second tutor, the more left-dominant they were when exposed to the first song [97]. Lateralized memory strengthens the performance of well-learned song and presumably enables the bird to be competitive for females in the coming season. Since magpies are improvisers and have no tutors [75], it is likely that the quality of learning and recall determines whether the sounds are stored in long-term memory (left hemisphere) [98].



**Figure 2.** Range of vocalizations expressed by Australian magpies. Range of vocalizations in the Australian magpie. These categories can roughly be subdivided as those that are a matter of affect, such as distress, fear and anger, but alarm calls, while also short, may involve forebrain regions (as in referential calls) or even in mobbing calls. Learned vocalizations in song, while not tutored, may have elements that are territorial or regional markers, and all mimicry is of course learned. Intentional vocalizations can be long or short, but they must have stereotyped characteristics, be uttered only in the presence of conspecifics and would usually lead to a change of behaviour in others (see [93,95]).

# 3.2. Song Control System in Magpies

When we sectioned magpie brains, albeit in a small sample (N = 9), we found that the female and male song nuclei of the magpie are about equal in volume and well developed and also well-developed in juvenile magpies (2–3 months post fledging), which is consistent with the vocal competence of juvenile magpies [99]. We also found the same song control nuclei and in the same topographical position in the forebrain of the Australian magpie, as present in canaries and zebra finches [50,52,99,100].

Our results indicate that, from juvenile to adult age, the volume of RA increases (10%), and the volume of the Area X decreases (19%). No such age-dependent change occurred in the HVC or LMAN (see Figure 1). The volume of mMAN (the medial magnocellular nucleus located adjacent to LMAN) was 40% smaller in juvenile females compared to a juvenile male and an adult female, but the volume of RA in the juvenile male was some 36% smaller than that of the juvenile females, suggesting that there may be both sex- and age-dependent differences in these nuclei. Interestingly, juvenile female magpies showed a fully-developed RA nucleus 2–3 months after fledging, whereas some RA was developmentally delayed in the juvenile males, and the reverse applied to the nucleus mMAN [99]. Since all of the measurements were made on coronal sections and only one side of the brain was measured, no data examining lateralization were collected.

# The Syrinx

The primary sound-producing organ in a bird is the syrinx, and the secondary system aiding sound production consists of the larynx, mouth, tongue and laryngeal muscles. Opening and closing of the beak may also affect the song produced [101–103].

The musculature controlling the syrinx is considered such a crucial anatomical feature that songbirds have been classified as such according to the absence or presence of these muscles [104]; or rather, the definition of a true songbird is based on the identification of the number of muscles present

in the syrinx. Some avian species do not have a syrinx and produce sounds via clavicular sacs, and suboscines may have a syrinx with just one or two pairs of syringeal muscles. Certain suboscines, e.g., Tyranni, such as pittas, have a mesomyodian syrinx with either no or just one pair of syringeal muscles [105].

In the true oscines, as are magpies, the syrinx is equipped with four or more pairs of syringeal muscles, typically five pairs, important in the production of song. More recent research suggests that the syringeal muscles have mainly a modulatory function [106]. Furthermore, as some writers about psittacine vocalization have pointed out, the complexity of sound and a rich vocal repertoire may belie the simplicity of the sound-producing apparatus [107].

In early 19th century studies of the function of the syrinx, it was assumed that both sides of the syrinx always act together to produce one sound; but since the development of spectrographs, it could be shown that this was not the case, and birds could produce harmonically unrelated sounds simultaneously on both sides of the syrinx, giving rise to the 'two-voice' theory of song. Nottebohm [25] lesioned the hypoglossal nerve leading to the left side of the syrinx of male canaries, the consequence of which was that the bird's song was severely affected, losing the majority of its syllables, but sectioning the right side alone had relatively little effect on the postoperative song, a finding that was confirmed by testing other small songbirds, such as several species of sparrow and chaffinch [50,108]. The experiments have shown that the neural control of the syrinx is lateralized, with the left side being dominant. However, to assume that neural control and physiological adaptations come only in a fixed model for all songbirds would be incorrect.

Birds vocalize by expelling air over the elastic membranes of the syrinx housed within the inter-clavicular sac, an air sac in the pleural cavity. In songbirds, the syrinx consists of two parts, one in each bronchus, and each is innervated separately [50]. For a long time, sound was seen as being produced by the actions of lateral and medial labia, as well as the medial tympaniform membranes in the syrinx (see Figure 3). The actual sound-generating mechanism, however, appears to be located in the lateral tympaniform membranes (LTM) and not, as believed in classic theories, the medial tympaniform membranes (MTM). Goller and Larsen [106] showed in his sample of songbirds (a female crow, *Corvus brachyrhynchus*, wild-caught male Northern cardinals, *Cardinalis cardinalis*, and brown thrashers, *Toxostoma rufum*) that even the removal of the MTM did little to alter song performance. Instead, they concluded on experimental evidence that, since sound production is always accompanied by vibratory motions of both labia, the vibrations of the labia had to be the actual sound source. The onset and termination of vocalization (called phonation) is usually controlled by the syringeal muscles that open or close the lumen on each side of the syrinx. The elasticity and complexity of the membranes may determine the quality of sounds. The air pressure, the muscles and the internal membranes can interact to produce near pure tones (single frequency and similar to human whistles).





Figure 3. Syrinx anatomy. The syrinx of *Gymnorhina tibicen* (A,D). (A) The first panel shows the exposed syrinx deep in the chest of the Australian magpie (requiring sectioning the sternum), autopsied and photographed by the author. The two lips (musculature) at the bottom of the image are at the point of dividing into the two bronchial branches. The syrinx is connected to the trachea and the bronchial tubes below, but at the most vibratory section, just above the thick muscle belt, there are sinews and ligaments. (B) shows the syringeal cartilage, dorsal view (as (A), of the European black-billed magpie, Pica pica, a relative in name only of the Australian magpie, which was named after the European magpie. However, both are songbirds and of about equal size. In Pica pica, the four tracheosyringeal cartilages are fused to form the tympanum. The photograph of the Australian magpie syrinx in (A) shows the trachea, the tympanum and the tracheosyringeal cartilage. Where the cartilage splits into its bronchosyringeal arms, this is covered in the photograph by a layer of muscle flaps (inversely heart-shaped). (C) presents a diagram of a syrinx (horizontal plane) of a male European blackbird, Turdus merula, one of the most common European songbirds, diverse and musical in its song. (D) is a histologically-prepared horizontal cross-section of a syrinx of an adult male Australian magpie prepared by the author. Note the similarities of details of (C) with (D). The syrinx of the blackbird and the Australian magpie is arranged very similarly, particularly in the medial and lateral labia, the lateral and the medial tympaniform membranes and the asymmetrical arrangement of the syringeal muscles [75,108,109].

The production of sounds depends on a number of additional physiological features, called the peripheral auditory system. The length of the trachea is important since formant frequencies are inversely proportional to the length of the vocal tract; i.e., if this were halved, the formant frequencies would be doubled [110]. Nowicki's paper of 1987 [111] showed that not just the syrinx, but the vocal tract contributed to the sound quality, at least in filtering sound [112], although, as a singular tube, it would not contribute to our understanding of lateralization, but can explain certain auditory characteristics [113,114]. Indeed, Hoese and colleagues [101] provided evidence experimentally of an important coordination between beak and sound output (Figure 4), showing that restricting beak movement or closed beak vocalizations [115] changed the tonal quality of song and caused frequency-dependent changes in amplitude that may alter the message and, thus, require some instructional cues from the forebrain, and these may indeed be lateralized.



**Figure 4.** Body postures for specific phonations/song types in Australian magpies. The bird (**A**) is producing a low-level alarm call; posture erect and vigilant, and head raised slightly, beak open. (**B**) The same bird quietly singing. Note the bird is erect, but relaxed, and the beak is closed. The arrow points to the laryngeal area, and movement of feathers is clearly visible while the bird sings. (**C**) A pair carolling (i.e., using the territorial call). The birds arch their backs, extend their necks and throw their heads back, opening the beak widely to produce this loud and specialized call; chest and belly feathers tend to be ruffled as if major muscle groups are also involved in sustaining the call. Body posture and beak movement thus substantially differ from postures adopted in alarm calls or song.

#### 3.3. Sound Production in the Magpie

Having identified the anatomy of the magpie's syrinx, our laboratory then proceeded to test phonation in wild magpies [116]. As in other songbirds, magpies have a tracheobronchial syrinx in which the cranial end of each primary bronchus contains a pair of vibratory structures, the medial and lateral labia, which vibrate in response to aerodynamic forces and produce sound when adducted into the expiratory airstream of the bronchial lumen (Figure 3 above). The muscles on each side of the syrinx are innervated by the ipsilateral tracheosyringeal branch of the hypoglossal nerve so that each side of the syrinx is under independent motor control by ipsilateral motor neurons that are in turn controlled by the central song system predominantly on the same side [116].

Lateralization of song production at the level of the syrinx (i.e., the contribution of the left and the right side of the syrinx) is relatively easy to ascertain either by syringeal nerve section or by measuring airflow on the left and right sides. If there is no airflow through one side of the syrinx, this indicates that the labial valve on the ipsilateral side of the syrinx is closed and silent. Vocalizations must therefore be generated by airflow through the contralateral side of the syrinx, and this was true of some magpie vocalizations, as described below [116].

We discovered during our investigation (see the details of the method in [116]) that in magpies, the left and right sides of the syrinx can simultaneously generate different, harmonically unrelated frequencies during some of these bilaterally-produced vocalizations. At first glance, this result fit into the 'two-voice' theory. However, in magpies, it was not a matter of syllables being produced on one side and some others on the other, but the distribution of activation was according to the frequency of sound. The higher frequency was consistently produced on the left side. The left/right distribution of frequencies explains why magpies can drop three or even four octaves of sound from one note to the next. Moreover, this lateralization of frequency range is in the opposite direction from other songbirds with very complex song or large repertoires studied previously, in which the right side of the syrinx produces the highest fundamental [116].

Another finding was that magpies sometimes sang syllables unilaterally while maintaining bilateral airflow through the syrinx. This motor pattern is rare in other songbirds so far studied, which nearly always silence the contralateral side of their syrinx during unilateral phonation [117]. The results also showed a number of nonlinear phenomena (such as biphonation, deterministic chaos, etc.) in which the two acoustic sources of the syrinx interact. Nowicki and Capranica [118] had found these in the black-capped chickadees, *Parus atricapillus*, and identified them as heterodyne frequencies (not harmonics), resulting from cross-modulation between the two syringeal sides. In magpies, we found such nonlinear phenomena in begging calls, and here, they were a prominent feature. Still, the workings of the syrinx in its detailed functions suggests that further investigation in species differences of lateralization may be important. Brenowitz [119] argued that revision may even be necessary especially for large songbirds or when songbirds with substantially larger song repertoires are being examined and concern the role hemispheric specialization may play.

Indeed, lateral specialization for different frequency ranges may, in fact, increase the range of frequencies that the bird can sing. There is some evidence of the advantages of lateralized control in so far as the magpies' patterns of syringeal lateralization are more similar to those in the brown thrasher, *Toxostoma rufum*, the grey catbird, *Dumetella carolinensis*, and the northern mockingbird, *Mimus polyglottos*, all of the family Mimidae, than to the motor patterns of other species that have been studied. In the northern mockingbird, two-voiced singing is achieved from a single side of the syrinx unlike the magpie's dual use of different frequency ranges on each side of the syrinx [120]. The comparison with the Mimidae species is useful because they are amongst the most prolific singers and thus invite comparison with the Australian magpie. We know of none of these prolific singers, including our own study, as to whether they are lateralized consistently in one direction or whether lateralization changes over time since the method permits only seven days of testing of awake and relatively confined birds. The thermistors that had been implanted were removed after a week and the birds released [116]. Perhaps even more important is the possibility that, if the syringeal activation is lateralized consistently in song repertoire.

#### 4. Testing Sound Perception and Laterality in Field and Laboratory Studies

So far, some of the areas of interest in lateralization in song/vocal production have been raised. The last section of this paper will now be devoted to auditory perception in magpies as gleaned from scores in field observations and some specific elements of foraging behaviour, pertinent to lateralization, discussed.

We have a good and representative sample of hearing ranges of non-songbirds, raptors and songbirds [121], and one can infer from the magpie's own vocalizations that their auditory range is likely to fit in well into the average range of hearing in songbirds so far tested (see Figure 5).

It is important to know this hearing range well because without this biological evidence, it would be difficult to argue for auditory perception and lateralization at extreme upper and lower ends of hearing capabilities, unless there is some evidence, as one of the following field observations will show. Audible sounds perceived by magpies may range from 0.5 kHz to 7 kHz, requiring higher sound pressure levels (SPL) for the very low frequencies (below 1 kHz), as well as for sounds above 5 kHz, at least judging by the range of sounds they can produce. At the low frequency end is a call that magpie females make. It is a particularly low frequency call emitted near or in the nest and typically directed at offspring (see Figure 5C). Its function seems to be both affiliative, as well as mildly punitive. The latter has been recorded in contexts when the offspring were still begging for food in the nest after the mother had fed them; a reassuring 'growl' (sometimes referred to as purrs) immediately stopped all begging (personal observation).



Figure 5. Magpie range of vocalizations. The figure shows the wide range of frequencies produced in magpie vocalizations, not included here is an actual song/warble sequence typically in the range of 1.5-2.2 kHz. y axis: frequencies in kilohertz (kHz); x axis: time in seconds. (A) is a complex single alarm call (type that is often a precursor to the eagle alarm call); ( $\mathbf{B}$ ) a sharp high amplitude alarm call; (C) a 'purr', discussed below; (D) is a mobbing call, containing a good deal of noise (grey); note that the mobbing call, stretched here for better visibility, has a characteristic midsection, which clearly distinguishes this category of call from alarm calls; that midsection being of less than 1 ms can at best be identified by a human ear as a faint 'click' sound, but with better temporal resolution of hearing in birds, it is likely to be unmistakable for conspecifics. Note that (A,B,D) are very high amplitude sounds, and (A,B) have frequency ranges (audible harmonics with considerable energy, darker horizontal lines/regular intervals) from 2 to 6 kHz and in some special calls, as (B), even maintaining some energy at 7-8 kHz. (C) By contrast, a very low amplitude 'purr' vocalization, is even lower (400-500 Hz) than the fundamentals of alarm calls and below the magpie's typical song and is usually delivered at 35–40 dB. Every example presents just one sound, but the darker harmonics indicate that the call has some energy at that frequency level, well above the first formant (A) at 6 kHz; (B,D) at approximately 5–6 kHz), and accordingly, one may assume that magpies can also hear most of the sounds they produce, even if the very upper limit harmonics (at 7 kHz and beyond) may become inaudible to magpies).

Anatomical differences between mammalian and avian audition have often been called upon to possibly explain differences in perception. Cohen [122] suggested that the hearing threshold of humans is generally about 18 dB lower than that of passerines, and the lesser hearing capacity in songbirds has been attributed to some main factors, although they have been questioned. King and McLelland [103] had shown that the basilar membrane of the cochlea of birds is restricted in size by head size. In pigeons, for example, this membrane is a mere 3 mm long, less than a tenth of that in the human ear. However, while this membrane carries the neuro-epithelial receptor cells, cells are far more densely packed in avian than in human ears, and so, King and McLelland [103] point out that the 'crista basilaris', in its cross-section, has about ten-times more receptor cells than the mammalian organ of Corti. A counter-argument made by Henry and Lucas [123] is that the avian middle ear has just a single ossicle, the columella, that transfers acoustic energy to the cochlea, while mammals possess three middle ear ossicles, and these ossicles improve high-frequency efficiency. Several studies of columellar middle ear systems indicate that efficiency is greatest from 2 to 3 kHz and declines sharply above 3–4 kHz (reviewed in [124]).

However, there is apparently another level at which avian audition is different and, in this case, arguably better than the human ear, and this is in the temporal resolution of sounds, which, according to King and McLelland [103], was alleged to be 10-times faster in songbirds than in human ears, but if true, would provide a substantial auditory advantage and possible specialized ability to focus on specific sounds. By 2002, a study by Dooling and colleagues [125] tackled this question of temporal resolution. They found that birds were capable of discriminations between two sounds that differed in fine structure over time intervals as small as 1 ms, much faster than any estimate of the monaural temporal resolution capacity of humans. The researchers were thus able to demonstrate that the temporal resolution in the processing of acoustic communication signals in birds was well beyond the limits typically reported for humans; with the correction of King and McLelland's [103] claims, however, that a bird's discrimination of the temporal fine structure of complex sounds is two- to three-times, not ten-times, better than the limits shown for humans [125]. Henry and Lucas [123] speculated that taxa with lower temporal resolution may compensate for this with greater frequency resolution. They base this on theoretical models of cochlear tuning that predicts a trade-off between temporal resolution and frequency resolution [126].

Whether or not any of these very specific aspects of audition in birds are lateralized remains largely unchartered territory. Studies in temporal resolution have been undertaken mostly on aquatic mammals [127]. Interest had also been particularly consistent with respect to localizing sound by establishing interaural time differences (ITDs) and interaural level differences (ILDs). The puzzle is how birds with small heads can identify the direction of sounds [128–130]. A more recent study suggests that budgerigars may be able to localize pure tones as high as 4 kHz based solely on ITD information and that small birds generally may be able to enhance directional hearing by using the acoustic coupling of the middle ear cavities and so perform well above expectations [131]. In larger birds, one suspects that head turning, studied in the context of visual perception, may be useful to identify sounds, and these could reveal side biases.

Indeed, several such studies of auditory laterality have been undertaken by placing the sound sources behind the test birds, some purely for establishing threshold levels [122]. The playback method, placing specific auditory stimuli to the side or behind an animal, is a technique that is usually used in larger animals as, for instance, a study on dogs that tested hemispheric specializations for processing auditory stimuli [132]. Dogs turned their head to the right side (left hemisphere) in response to conspecific vocalizations, but to the left side (right hemisphere) in response to the sound of a thunderstorm. In birds, because of their small heads, it usually becomes a little more difficult although not insurmountable to test auditory responses. One study, for instance, tested experienced and young, inexperienced harpy eagles and exposed them to sounds of pure tones, of a bird (tinamous) and of a potential prey item (howler monkey calls) and of a conspecific from a speaker placed behind the bird. Both young and adult harpy eagles turned their head to the left when exposed to irrelevant sounds, such as pure tones or peeps of the tinamous, and both turned right on hearing the calls of another harpy eagle. On hearing the calls of the howler monkey, however, the captive young harpy eagle without hunting experience oriented to the left, whereas the eagle experienced in hunting oriented significantly to the right, clearly an example of purely auditory orienting asymmetry [133]. This suggests that socially-relevant information and potential food items are identified by sound alone and processed by the left hemisphere.

In humans, a behavioral method used to establish hemispheric dominance in auditory perception is dichotic listening in which subjects have earphones in both ears and similar sounding consonants (such as Da/Ta) are delivered to each ear separately and simultaneously, and the subjects then tell the experimenter which consonant/syllable they mostly heard. Research in those cases have shown a clear right ear/left hemisphere dominance [134,135].

The same method (in principle) has been successfully employed in studying the ability of budgerigars to identify cues of interaural time differences (ITDs) and interaural level differences (ILDs) by implanting headphones [131], a technique also used to test left-right identification of sounds [136]. Interestingly, in humans, ITD performance drops off markedly for frequencies above 1.5 kHz, but budgerigars maintained sensitivity up to 4 kHz. The method could be used to also establish ear preference. Possible methods of auditory lateralization testing for lateralized brain functions have recently (2017) been discussed by Rogers and invite further study [137].

#### 5. Field Studies Concerning Audition in Australian Magpies

#### 5.1. Introduction

Very few field studies have shown lateralization of auditory processing in birds. There has been one study that meticulously established that some prey search by magpies is based purely on audition. Floyd and Woodland [138] hypothesized that magpies can forage for scarab larvae purely by listening to the chewing sounds they make in the soil. These sounds are so faint that the experimenters were unable to hear what the magpies heard under the same field conditions.

Magpies feed regularly on scarab larvae, and they are a prized food owing to their size (2–3 cm) and the high protein content and fluids they provide. Some studies confirmed that, in some cases, grubs retrieved from below the surface could be found by visual means. In heavily infested areas in England, rooks, *Corvus frugilegus*, and starlings, *Sturnus vulgaris*, feeding on scarab larvae, *Phyllopertha horticola*, were able to do so because of visual cues, for instance when turf had died off, i.e., had changed colour, or the soil surface was loose and could be lifted and pulled aside [139]. The American robin, *Turdus migratorius*, was also shown to use visual surface cues (worm casts) for locating earthworms [140]. Similarly, it was known that in Australia the currawong, *Strepera graculina*, closely related to the Australian magpie, both belonging to the family of Artamidae, used a similar visual guidance system in years of severe infestation of scarab beetles of the species *Seriesthis pruinosa* [141].

However, not all scarab larva species leave identifying marks on the surface. Floyd and Woodland [136] wanted to know how magpies could find larvae that leave no visual cues. First, they established that there were no visual or other cues by which the magpies could identify where the larvae were, and they then conducted a series of auditory tests, finally pre-recording the chewing sounds the larvae made while feeding underground and playing back these sounds to magpies through micro-speakers. Under well-controlled experimental conditions, they could then test whether the magpies found the sound source. They did.

The speakers they used for playback in the field had a frequency response of 50–12,000 Hz [138]. Most of the sounds played backed to the magpies were at frequencies between 50 and 800 Hz, but there was a small high frequency component in the 1700–3000-Hz range. The scarabs produced sounds at an intensity of 30–38 dB. As tape hiss intensity was 30 dB, the subjects were offered a choice of playback of scarab noises or tape hiss alone (at 30 dB); the former resulted in immediate and successful responses; the latter did not elicit responses. Playback intensities were measured at 2 cm above ground level [138].

#### 5.2. Foraging for Scarab Beetles by Magpies Is Lateralized

My own field observations on foraging behaviour in magpies (specifically for scarab larvae) are based on recordings made over a three-year period using several of our well-established research field sites on the Northern Tableland, near the city of Armidale, New South Wales (30°32′ S, 148°29′ E). All sites were permanent magpie territories of 3–7 residents, consisting of one breeding pair, juveniles and also some young adults (daughters from the previous year). Each territory was at least 2.5 hectares in size, flat grassland dotted with the occasional mature gum trees, some pine trees and shrubs, an environment in which scarab larvae flourish. Two of the territories were adjacent to each other while the visits to two others were separated from each other by at least 2 km and 5 km, respectively.

On this Northern Tableland, largely sheep-grazing country, at altitudes of about 1000 m, three species of scarab beetles were strongly represented [142]. The larvae may pupate and emerge as beetles any time between November and March, i.e., larvae reach their full size at exactly the time when magpie offspring fledge (around September, sometimes earlier-depending on weather conditions) and make the greatest protein and food demands on the parent birds.

Magpies feed exclusively on the ground, and they walk, putting one foot before another, while foraging, sometimes referred to as 'walk-foraging' [143]. Their ground feeding habits make them easy to watch and follow their foraging in open fields especially. Moreover, magpies forage very systematically and according to a time-plan. They will reliably be at one specific transect of their territory at a certain time of day and will generally walk diagonally and in half a meter to meter distance from one another (Figure 6). No matter how large the territory, once their habits and time frame were known, observations could be made at set times in the morning and in the afternoon (changing the hour of day weekly to cover the times of their most vigorous foraging in the morning and the later afternoon).



**Figure 6.** Directionality and spacing in magpie foraging. Magpies tend to walk slowly and steadily in a direct line and in parallel to each other, taking transect after transect in a methodical way.

Each territory was visited daily for five days a week between September and March for three consecutive seasons, and all observable incidents of extractive foraging were recorded. Individual magpies could not be identified.

In the first weeks of watching foraging behavior closely, it became clear that the steps in all successful extractive foraging events were the same; the foraging bird was: (1) scanning the ground walking slowly; (2) then stopping and seemingly looking closely at the ground binocularly; (3) holding absolutely still; (4) in the last moment, turning the head so that the left side of the head/ear was close to the ground; (5) straightening up, the bird then executed a powerful jab into the ground; (6) then retrieving a large scarab larva from the grassy surface; and (7) expertly removing the hard head and the biting mandibles before swallowing it or feeding it to an offspring. Steps 3–7 typically lasted less than 30 s.

# 5.3. Results: Extractive Foraging

The sheer consistency of the foraging sequence and the changed posture of the bird observed made it possible to recognize the special extractive foraging strategy and made it clear, especially in

some years with greater abundance of scarab larvae, that this was not an unusual and rare event, but a seasonal and integral part of the foraging behaviour of the territorial magpies, at least in a region where scarab larvae were often abundant.

A total number of observations accounted for 446 attempts at extractive foraging, but only 135 observations were ultimately included. One reason for the exclusion of a substantial number of seemingly successful extractions was the consequence of the behaviour of juveniles. Young juveniles (a month old or less post fledging) walked with the parent bird, but had the tendency to intervene in the process of foraging, by posting themselves in front of the adult to block the path, just so as to ensure that the morsel was fed to them as shown in Figure 7.



**Figure 7.** Parent feeding scarab larvae to magpie juvenile. Female magpie feeding a larva to a young fledgling. Such an example was not included in the analysis, and this method of feeding, the juvenile right in front of the parent bird, was limited in time and dependent on the juvenile's development. Blocking the way and front of feeding was observed only in juveniles one month post-fledging. By two months post-fledging, most juveniles walked next to the adult (usually on the right side) and actively started observing the processes of the adult's food acquisition.

The most common reason for exclusion, however, concerned problems for the observer regarding distance or terrain. The most obvious problem occurred when the magpies foraged with their backs turned towards the observer and often at some distance, and in such cases, it made it difficult to be certain of the direction of head movements prior to extraction. Hence, such sequences were excluded even when the actual retrieval of larvae was seen.

The instances included were based on the foraging data obtained from four different territories. In an area of over 18 hectares traversed daily, the total number of resident magpies observed seems small (N = 16), and hence, it is very possible that, in some cases, the same magpies were scored repeatedly if they happened to be the successful ones in extracting the larvae, and this may partially account for the consistency of the findings. Relatedness is unlikely to be an issue in these results since juveniles forced out by the parents tend to roam in bachelor groups for at least four years and feed in non-dedicated, usually inferior, sites before some of them succeed in finding a suitable territory and a partner. There is no evidence that a daughter or son might secure a neighbouring territory.

Equally, the number of juveniles observed, at least in the first month of the season (September), typically made no contribution to extractive foraging, but were keen consumers: they often did not commence making successful extractions of larvae on their own until nearly the middle of the observation period. Hence, although some magpies may have contributed several scores of extractions of larvae over the observation period of three months, this does not invalidate the observations because

each event was a new event and an individual magpie could have approached the excavation site differently on each occasion.

Most incidents of successful extractive foraging were observed in October and November, the observed incidents sharply declining after mid-December when the ground became very dry and compacted and most scarab beetles might have emerged (see Figure 8).



**Figure 8.** Walk-foraging and successful extractive foraging events. The majority of scarab larvae were retrieved in October, decreasing substantially by December and found only scarcely thereafter and not at all by February (percentage figures refer to successful retrievals counted). The large light-shaded semi-circle shows the months and hours when juveniles started searching for scarab larvae on their own, mostly with relatively little success.

All 135 recorded sequences showed the same left ear preference: the bird being observed tilted the head so that the left ear was held closer to the ground before straightening up and delivering the successful jab of its beak into the soil (Figure 9). This tilting of the head to a left position was clearly visible in each of the incidents. One would expect to find that not all scores of extractive foraging used the left ear (i.e., at least some magpies might have tilted the head in the other direction), but this was not so. Even though some of the scores were likely repeats for the same individual, the total absence of right ear use means that the bias is significant at the population level.



**Figure 9.** Lateralized auditory detection of prey item. The image of the magpie shows Step 4 in the extractive foraging sequence, moving the head from a 90° angle, binocular viewing, to a 45° angle, moving the beak to the right and up so that the left ear is closer to the ground.

# 5.4. Discussion

To my knowledge, this is the first example of auditory lateralization in the field describing an extractive foraging event that has not been described in any avian species. It is also the first example of auditory behavioural asymmetry under natural conditions.

The point made here is that the foraging strategy was not based on visual scanning, but crucially on auditory examination of a potential prey item and that it was consistently performed by the left ear. In the image shown above (Figure 9), the bird is walking leftwards, and the right ear would have been nearer for auditory inspection than the left, but the bird turned the head right around in order to listen to the underground larva with its left ear. In all cases included in the sample, the birds turned to position their left ear close to the ground.

It seems highly unlikely that this head tilt related to improving visual scanning. The visual field of magpies in the binocular field at close range is about 28–34° [4], and any fixation of a potential prey item is therefore most accurate when the beak points at about 90° to the ground (for binocular viewing). Since scarab larvae create no visual surface cues, as Floyd and Woodland (1981) had so convincingly shown [138], the only way magpies are able to identify the location of the underground prey item is by auditory means. Hence, regarding the head tilt prior to grasping the grub, we are left with only one explanation, namely that the bird obtained confirmation of the presence of a scarab larva exclusively by aural means.

In retrospect, watching magpie groups combing through their territories in such an orderly fashion (Figure 6 above) and doing so grid-by-grid every day may well be a result of having acquired the skill of extractive foraging. Clearly, the sounds that larvae make are so faint that they would be easily missed unless a group spaces out in such a way that every part of the ground can actually be scanned by listening to sounds at very close proximity.

# 5.5. Additional Field Results in Magpie Foraging

The results of foraging raise the question why this auditory behaviour is left-biased (right hemisphere) and significant at the population level and how this may fit the results in other and related studies we had conducted.

The extractive foraging results of lateralized listening follow from the results obtained on lateralized foraging behaviour in magpies in a series of additional field studies conducted by members of our laboratory [4,144]. One tested head turning during foraging (visual scanning); another scored eye preferences for tracking moving prey (for both, see [4], called Study 2 in the summarizing table below); and a third scored the side of begging behaviour of juveniles walk-foraging with a parent bird [144] (see the results summarized in Table 1 below).

Head turning during visual foraging (pecking food from the ground) was found to favour the right eye/left hemisphere. There was a slight, but significant bias at the population level for the bird to turn its head so that the right eye monocular field was directed towards the ground.

In a third study (eye preference for moving prey [4]), we supplied the magpies with food by purposely throwing mince-meat pieces in their direction and then scoring which eye they last used before taking and consuming it. Of 155 scores, 97 percent were left-eye dominant, meaning they involved left-eye viewing the moving target before food retrieval.

Later that year (also published in [4]), we had the opportunity to observe magpies dealing with moving prey items and watching the magpies trying to capture them. There was a locust plague, and locust were either jumping or flying up from the grass. Under natural conditions, we received the same results as in the food-supplementation experiment, finding a strong left-eye/right hemisphere preference. The results are consistent with use of the right hemisphere processing spatial information as known from studies in chicks [145].

In another field study (called Study 4 here; see also Table below [144]), it was recorded on which side juveniles approached the parent birds and begged for food while walk-foraging, and a significant group-level bias for begging on the right side of the parent was found. Juveniles were 2.46-times

more likely to beg on the right side than on the left [144]. By begging on the right side of a parent, a juvenile uses its left eye to view the adult and is in the parent's right visual field. Hoffman et al. [144] pointed out that visual inputs from the right visual field are processed by the left hemisphere, which is known to inhibit conspecific aggression, as found in chickens [146]. By approaching in the right hemifield, a juvenile magpie may also avoid being scolded by the parent bird [144]. Alternatively, and more likely, as a recent comparison across species indicates [147], the infant is positioning itself so that it can monitor the parent's behavior using its left visual field and right hemisphere, specialized for processing social behaviour.

Study	No. (Subjects)	No. Scores (Behavioral) Total/Bracket: Majority of Responses	Left Eye or Ear/Right Hemisphere	Right Eye or Ear/Left Hemisphere	Authors
(1) Extractive foraging	16	135 (135)	Left ear dominant		Kaplan, this paper,
(2) Head-turning during foraging	20	266 (116)		Right eye dominant	Rogers and Kaplan 2006 [4]
(3) Tracking moving prey	12	159 (155)	Left eye dominant		Rogers and Kaplan 2006 [4]
(4) Begging position of juveniles during foraging	6 parent-juvenile pairs	16/64 scores	Left eye dominant (begging juveniles)	Right eye dominant (feeding adult)	Hoffman et al. and Rogers 2006 [144]
(5) Inspecting predator	55	270 (compound score/various behaviors)	Left eye dominant		Koboroff, Kaplan and Rogers 2008 [148]

Table 1. Hemispheric specializations in five field studies on foraging and vigilance in magpies.

Brackets give the number of subjects/behavior showing eye/ear bias.

A fifth field study, not on foraging, but on eye preference in magpies when viewing a predator, scored eye use when presented with taxidermic models of a potential predator, a lace monitor [148]. We established by scoring monocular fixations from video footage that magpies used their left eye in the majority of instances while inspecting the potential predator, such as jumping (73%), prior to circling (65%), as well as during circling (58%) and for high alert inspection of the predator (72%), and we concluded that mobbing and perhaps circling are likely agonistic responses controlled by the left eye/right hemisphere [148].

The results of the second field study are consistent with preferred use of the left hemisphere and right eye in control of feeding responses as has also been shown in other species, including the zebra finch [149]. In the third field study, magpies show a right eye/left hemisphere preference reflecting a specialization for spatial information using global cues and also for rapid responding. It is thus noteworthy that of the three foraging tasks, two were controlled by the right hemisphere or expressed differently; it would appear odd that two foraging tasks looking for prey on the ground and looking for prey under the ground are managed by different hemispheres. The reason for this becomes clear in this context: one is consistent with feeding responses generally, while the other method (extractive foraging using the left ear) is based on spatial information and auditory cues. Hence, these two foraging methods do not just require different strategies, but are under the control of different hemispheres. While three of the findings for four field studies relate to visual lateralization in magpies (see Table 1), there may also be an auditory element to them.

My field study of foraging for scarab larvae showed a very strong bias towards the left ear to pinpoint the larvae's presence under the ground, leaving the right ear free to respond to the begging or other calls of an offspring. This may allow the magpie to attend to two tasks at once. Rogers et al. [148] showed in chicks that the performance of two tasks simultaneously, such as foraging and attending to a predator overhead, is undertaken effectively in strongly-lateralized chicks in which visual search is processed by the left hemisphere and predator detection by the right hemisphere [150].

Furthermore, agonistic responses are processed by the right hemisphere, consistent with research results in chicks [146] and other species [151]. Chicks also use the left eye to examine novel objects and the details of a stimulus detecting small changes in familiar stimuli, whereas the right eye detects large changes that represent categories rather than details [152]. It is conceivable and even probable that the same hemispheric specializations that apply to eye use apply also to ear use.

# 6. Conclusions

This paper has presented evidence of lateralized behaviour in phonation and listening in one songbird species. Motor output and the way magpies produce song were shown to involve an entire range of techniques that enable an individual magpie not only to maintain singing for hours, but allow for a range of extraordinary modulations at a wide range of frequencies by using unusual techniques of lateralized frequency use (higher on left, lower on right side of syrinx). Paradoxically, so far, specific functions for their varied song have not been discovered. It is clear that their song can identify individuals one from another [75], but such individual recognition is conceivably achieved by just listening to their territorial call, referred to as carolling. There appears to be no territorial advantage for having a larger or smaller repertoire. It is possible, given that magpies form auditory maps of other species in their territory (they mimic only heterospecific sounds pertaining to their territory memory, in this case of heterospecific sounds, is lateralized on the left side, as in other songbirds, but this has not been studied. It is also possible that such auditory 'maps' may be linked to other brain regions.

The substantial and innovative neuroscientific research in avian vocal production and vocal perception over the last decades notwithstanding, it pertains largely to a few small songbird species. Ocklenburg and Güntürkün in their paper [153] published a telling 'cladogram' showing that we have no information at all on lateralization in vocal production (central and peripheral) and vocal perception on any of the 28 clades of extant non-songbirds. Although Passeriformes are just one clade in this cladogram [153], Passeriformes, i.e., the true songbirds, actually make up the majority of all extant birds (over 5000 species). Additionally, while we know plenty about the zebra finch and a few other songbird species in this regard, there is little to no information available on almost all other extant songbirds either. It would help to understand whether large repertoires and flexible/plastic brains have developed other or additional neural mechanisms for song production and perception and whether this is achieved via specific hemispheric specializations. The magpie is certainly a representative of this kind of songbird. With an evolutionary history of likely more than 20 million years and in an evolutionary context of substantial speciation pre- and post the mass extinction of 65 mya, the emergence of a major songbird at that time may be as fascinating genetically as it is in its current performance.

Here, results of several field studies were presented. The results of lateralization in the field have been telling us that there are behaviours that are clearly highly lateralized in magpies. Extractive foraging has a particular place in ethological-cognitive research and, in primates, has been identified as one of the very complex cognitive behaviours and, when reported, relies usually on vision or on experience, but not purely on audition (the very specialized adaptations of the aye-aye being one of the few known exceptions).

This is the first paper that reports this auditory behaviour in a songbird and, furthermore, shows that the success of it may depend on a highly lateralized neuronal aspect in the auditory system. The results of the other field studies on foraging behaviour make a powerful point that the bird has to handle very different experiences and tackle potential dangers while foraging or encountering predators. Here, it has been shown that these key functions are lateralized, which may have substantial advantages for survival.

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