Original Communication

Babbling in a bird shows same stages as in human infants: The importance of the 'Social' in vocal development

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ABSTRACT

Over forty years ago Marler asked whether there might be parallels between birdsong and human speech development and, indeed, neuroethological studies have since confirmed important (convergent) similarities between songbirds and humans in brain function for vocal learning. Yet little concrete evidence exists of the behavioural expression of the first stages of vocal development demonstrating similarity between babbling in human infants and songbirds. Uniquely, Australian magpie nestlings and juveniles have been found to incorporate approximations of human speech and words in their early repertoire practice. Because these sounds are clearly identifiable and recognisably different from their species-specific song, this offers a window for discussing mimicry in the context of infant language development. This paper will report and analyse pre-human mimicry segments (i.e. a bird's mimicry of human speech prior to the development of individual and identifiable human words) in early expressions of general vocal practice in nestling and juvenile hand-raised songbirds. The data derived from vocal records demonstrate that phonetic play follows patterns similar to human babbling. This exciting discovery demonstrates that, under certain conditions, the acquisition of song follows stages of phonetic play. These correspond roughly to human language development, and also raise the question of the role of vocal mimicry. This finding perhaps even suggests evolutionary constraints on language acquisition.

KEYWORDS: babbling, birdsong-human speech comparison, vocal learning, mimicry.

1. INTRODUCTION

This project documents in detail the vocal development of Australian magpies, *Gymnorhina tibicen*, a relatively large-sized songbird (Fig. 1) with a substantial and melodious repertoire, known also for its ability to mimic [1]. In this sense this species is a powerful alternative to investigating song learning. The majority of studies in vocal learning have been undertaken in birds with fixed, male only and seasonal song, such as the zebra finch [2]. Vocal learning in such songbirds has taken on model character for the study of human vocal development and many comparisons have been made between the development of birdsong and human speech [3-6]. By contrast, magpies, as a species, have credentials similar to humans in that they have a plastic brain capable of ongoing learning and both males and females sing, i.e. song is species-specific rather than male-specific and not tied to reproduction. It was hypothesised that these factors, despite evolutionary distance, should have specific merit and might even reveal similarities between vocal development in this species and in humans.

1.1. Vocal learning

A very select group of species and orders can learn vocalisations. There is documented evidence that some cetaceans [7] and seals [8], as well as elephants [9, 10] and bats [11] have some limited capacity for vocal learning. But these so far remain isolated cases amongst mammals, with the exception of humans. Songbirds, however, and also hummingbird species [12, 13], form a very large contingent of vertebrates in which vocal

Adult Australian magpie

Fig. 1. Male magpie *Gymnorhina tibicen*. This species has no taxonimic relationship to the European black-billed magpie (*Pica pica*). There is very little dimorphism between the sexes. The male is identified by clear white feathers on neck. The female has a little grey rim at the nape of the neck that is otherwise also white.

Song control system

Fig. 2. Lateral view of avian brain showing the nuclei involved in song (longitudinal section). This is a very simplified schematic version of the song control system [31] (after Doupe and Konishi, 1991) in the brain of the adult male zebra finch. Black nuclei represent descending motor pathways. (HVC, high vocal centre; RA, robust nucleus of the archistriatum; nXIIts, tracheosyringeal portion of the hypoglossal nucleus). The shaded area identifies a second pathway to link HVC and RA: from HVC to area X to DLM (the medial nucleus of the dorsolateral thalamus) then to LMAN (lateral magnocellular nucleus of the anterior neostriatum) and from there to RA. Field L, in grey, is the primary avian auditory area which projects to RA and HVC (see also [32] for more detail).

learning is the norm, and the ability of complex vocal learning has also been shown in parrots [14-16]. According to Sibley and Ahlquist (1990) [17], songbirds, parrots and hummingbirds are, in fact, not closely related taxonomically leading Gahr (2000) [13] to suggest that vocal learning may have evolved independently at least three times among birds.

1.1.1. Brain circuits

The avian forebrain does not share the layered structure of the mammalian cortex but, as has been argued, it has many of the same functions, in particular those known to involve higher cognition [18]. This point is modified by Güntürkün and Bugnyar (2016) [19] who argue that, while there is an undeniable convergence of several neural mechanisms for cognition and complex behaviours, the overall forebrain organization tends to be vastly different between birds and mammals. Many theories on vocal development draw on a close association between behaviour and neuroscience [20] since behavioural development is dependent on physiological and neural processes. Sound production in songbirds depends on the vocal apparatus and its development: full song is produced only once the syringeal muscles have fully developed [21, 22]. There are also neuronal
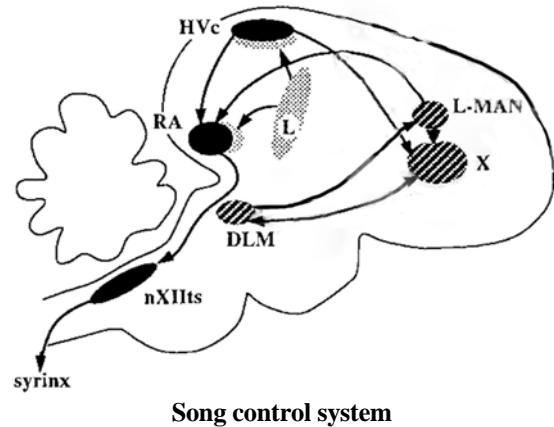
prerequisites for song and some of these grow, alter or are subject to transitional stages during development. Centrally, song learning is associated with memory formation and the neural apparatus to support long-term memory of song. Research on vocal development is thus situated in several disciplines. Not all songbirds or parrots share the same vocal plasticity, however, even as juveniles, let alone as adults. As far as we know today, only a small number of songbirds, but a large number of parrots are life-long learners [23].

Much of the extensive research on vocal learning and vocal development has focussed on small songbirds such as in zebra finches [24-26] canaries [27, 28], sparrows [29], or white-crowned sparrows [3, 30]. Such studies have resulted in detailed neuroethological knowledge and a map of the song control system of birds (Fig. 2) as well as in studies on the syrinx, the sound producing organ located deep in the chest at the bronchial bifurcation.

Recent studies have placed the emphasis on questions of the essential acoustic features of information transfer. Rose *et al*. (2004) [33] have shown in white-crowned sparrows, *Zonotrichia leucophrys*, that song learning can occur on the basis of being exposed only to phrase-pairs. They tested this by providing a sparse sequence of vocal information of the template necessary for generating a complete song. They found that the sparrows were able to learn the complete song from these 'snippets' of information. However, their findings also suggested that there is a minimal requirement of sequence information because when a control group was exposed to all species-specific song elements but each of those elements was presented singly (rather than as longer sequences or phrase-pairs) they failed to develop normal, full song. It has also been shown that deaf birds, deprived of feedback signals, cannot correct errors [34], although there appear to be some exceptions [35]. Nonetheless, zebra finches are thought to possess an early auditory bias in favour of their own species-specific song [36] demonstrating that auditory constraints can channel vocal learning. Gobes and Bolhuis (2007) [37] showed that tutored-song memory and a motor program for the bird's own song have separate neural representations in the songbird brain and thus confirmed that biological/inherited propensities exist alongside malleable environmental input even in birds with relatively simple song or relatively few song types.

1.1.2. Vocal learning as a social behaviour

In behavioural research, great progress has been made in identifying essential criteria for the successful learning of song. Particularly in tutor-guided song acquisition, the quality and extent of social facilitation in song learning has been investigated. As Galef (1998) [38] stressed, social learning refers to acquisition of information from conspecifics and this facilitates development of adaptive patterns of behaviour. In several species, it has been shown that the quality and type of tutor can play a decisive role in the shaping of song of an offspring and that juveniles also appear to make choices from whom they will learn [39, 40].

Research into acquisition of song has also shown that the concept of learning purely by exposure to the acoustic aspects of song may be incorrect since cues are rarely mono-dimensional but, rather, many-layered. Social interaction during the sensitive period is often required [41]. Adret (1993) [42] has demonstrated that visual stimuli (in the form of video images) have reinforcing properties for learning of song by zebra finches. Hultsch and colleagues (1999) [43] have also shown that stimulus pairing of auditory and visual cues enhances perceptual learning of song in nightingales, *Luscinia megthynchos*, leading to more accurate copies of the song as well as to a larger song repertoire. In other words, hearing song while seeing the tutor singing enhances neural activity in those regions of the forebrain known to be essential for song learning.

Auditory experience usually includes sounds not specific to a species and one can argue that certain social environments may encourage the development of mimicry. It seems now more certain that, in some cases, mimicry may confer some advantages or even have specific functons [44-46]. Since it is now known that at least 15% of birds worldwide can mimic [47], mimicry has spawned extensive research and has continued to generate substantial theoretical interest [48].

Since the discovery of mirror neurons in birds by Prather and colleagues (2008) [49] we also know that birds can learn song without being actively supervised and instructed by an adult. Tchernichovski and Wallman (2008) [50] explain that the bird obtains a copy of the song in its memory against which it can judge its own output (performance) of the song, which is an invaluable finding for song development in species that learn song without active tutoring by an adult, i.e. for avian species that are improvisers, and for those that do not use song for mate choice and/or are not sexually dimorphic in song production. The Australian magpie is an example of all these criteria. Kroodsma *et al*. (1996) [51] had warned some 20 years ago that negligence in considering songbirds such as those of the Southern Hemisphere may lead to the omission of important topics.

1.1.3. Vocal learning in comparison with human speech acquisition

Marler's classical study (1970) [3] of teaching white-crowned sparrow juveniles, *Zenotrichia*

leucophrys, to sing by listening to playback of tape-recorded song showed that learning is limited to the first 50 days of life and this established the concept of a sensitive period in song learning, inspiring other researchers into further research on the importance of the sensitive period [52]. Clearly, vocal development in both birds and mammals is considered as more than merely a passive process of maturation of motor and memory abilities [53] and it was recognised early that vocal learning in songbirds may be a very good model to understanding human vocal/speech development.

Human babies are said to preferentially attend to speech sounds [54] and young songbirds may be predisposed to paying particular attention to the vocalizations of their own species. It has been shown that vocal motor development proceeds in stages. Young individuals begin by making vocal sounds that do not resemble those of adults (babbling or early subsong) and develop showing effects of auditory experience at the next stage of vocal development [6].

The problem of comparing human vocal development with the vocal development of birds is that zebra finches and similar model species are sexually and vocally dimorphic. Relatively little is known of song acquisition, song production or memory formation and retention in those passerines for which these sexually specific conditions may not apply [51]. In particular, rather little attention has been paid to passerines that do not use song for mate choice and passerines that are not sexually dimorphic in song use. Instead of crystallised and limited song repertoires as in zebra finches, there are indeed many songbirds that have vast and flexible repertoires [55] and some of these live in permanent social groups or neighbourhoods, contexts in which brain plasticity might be a prerequisite or at least a distinct advantage. Australian magpies belong to this latter group. Moreover, they are capable of vocal learning throughout their long lives (lifespan of 25 to 30 years). As explained in great detail elsewhere [56], magpies have very large repertoires, males and females not only sing alike but have the same song control system [32] and are very accomplished mimics. All these factors make them highly suitable candidates for comparative studies with human speech development.

In this paper, some of these interrelationships will be demonstrated in the vocal development of the Australian magpie, one of Australia's foremost songbirds. Against the background of general vocal development, a very unique situation arose and offered the opportunity to study not only normal vocal development but also, from babbling state onwards, the development of mimicry of human speech in magpie nestlings from the first week post-hatching to 7 months of age, to a time when vocal performance tends to equal that of adults although the repertoire can change and expand throughout life.

1.2. Mimicry

In studies so far undertaken, quite a few have found specific functions but whatever has been found so far has been specific to that species, but none hold universally for all avian species. There is ample evidence that many song birds mimic and some of them, such as the migratory marsh warbler, *Acrocephalus palustris*, [57] and the European starling, *Sturnus vulgaris* [58], may well hold records for producing the largest number of identified mimicked sounds. Some 113 species are mimicked by male marsh warblers and as many as 11 orders of birds by starlings, including also the vocalisations of mammals and the sounds of inanimate objects [59]. Alec Chisholm was the first to list 56 Australian avian species as having some ability in mimicry [60]. Since then about half of the ones that he named have been verified.

Vocal mimicry is so far known to occur only in birds, some cetaceans and seals, as well as in humans [61, 62]. At the very least, encoding of sounds of another species suggests some facultative responses, meaning auditory learning, and so mimicry can have a role to play in exemplifying vocal development and learning. This was the conclusion drawn in a paper on call mimicry by eastern towhees [63]. Vocal mimicry is thus of great interest because it is can deal with the universal question of how vocal learning is achieved [64, 65].

Mimicry is only a small subset of sounds within the wide repertoire of Australian magpies and one might dismiss this as being of little consequence for the life of magpies and hence of little research interest. We know of magpies that mimicry is

present all year round and is performed by both sexes [66]. The number of mimicked sounds so far known to occur in magpie song well exceeds that known for the vocalisations of 20 other avian species, and it includes mimicry of the calls of nocturnal predators (such as owls), and a range of mammals, foremost dogs and horses [67, 68]. Magpies have also been reported to give imitations of the human voice and to whistle in an almost human fashion [68, 69]. Since magpies do not use song during the breeding season, the presence of mimicry in juveniles and adults is all the more intriguing.

2. METHODS

There are many recorded observations about the vocal repertoire of Australian magpies [68, 70-72]. However, developmental studies are more or less entirely absent. In other words, this study had to proceed from a series of unknowns. It was therefore necessary to

1. Establish normal physical and vocal developmental phases in wild-raised and hand-raised magpie nestlings and juveniles.
2. Hand-raise orphaned magpie nestlings and compare their development with that of wild-raised birds.
3. Analyze vocalizations and identify elements that get dropped, remain or develop over time.
4. Actively attempt to teach magpies human words.

2.1. Observing nest sites

Three nest sites of free-living magpies were selected for in-depth observation with observation periods of 2 hours per day. Observations were conducted from as close to the time of hatching and throughout the entire four-week nesting period over three separate breeding seasons, including two of the same pair and one of a new pair in each respective year. Nest sites were at a height of 6-10 m above ground level.

One nest site was located within the experimenter's property and, in this case, for the 4 weeks of nest occupation, the nestlings' vocal utterances were recorded from dawn to dusk and these free-living magpies, once they had fledged, could then also be observed and recorded for a further seven months on the same property.

Not one wild-living pair in this sample raised more than two offspring in a year (although up to four may be raised by a pair) and in almost all cases, only one was raised per year. Over 3 years of observation, the free-living magpies successfully raised 13 nestlings (2 per year, N = 6, from the resident pair on the author's own 3 hectare property alone). The greater success rate in raising offspring of the magpies on the experimenter's property may be attributable to a number of factors such as the absence of cats and of most predators generally, the presence of higher and more foliated (protected) nesting trees, and possibly the quality of the territory.

2.2. Housing

Hand-raised birds used for this study (N = 12) arrived as (orphaned or injured) nestlings and had to be fully raised from nestling to juvenile dispersal age (7-9 months) or until the bird itself chose to disperse. Every care was taken not to disadvantage hand-raised magpies compared to their wild counterparts. Hence, all hand-raised nestlings were placed in nests at 1.8 m height in a large outside aviary covered above by a 4-metre high transparent roof and a natural substrate of soil and grasses, with plants and a view to the native garden. Wherever possible, i.e. when nestlings were the same age (important because of synchronous hatching), as many as four nestlings were raised together in one nest and one aviary. Only in two cases this was not possible and each nestling was raised singly in separate years, turning the initially planned 3-year study into 5 years. The decision to raise the singletons separately turned out to be of major significance as the results will show. Providing near-naturalistic conditions for the maintenance of a captive group of animals is not only beneficial in terms of animal welfare but also, ultimately, for research. Well-nourished, responsive and non-stressed animals are more likely to show behaviours that follow normal developmental trajectories than do deprived animals. However, to ensure that this was not just an assumption, the hand-raised youngsters were always compared (simultaneously) with free-ranging groups of the same age. Feeding times, for instance, were copied from the free-ranging parents leading to an unrelenting schedule of feeding every ½ hour whilst in the nest and every 1.5 hours once

they were branchlings (with larger portions delivered). Water was not provided while magpies were nestlings or branchlings but at least once a day a food item was injected with an extra 0.2 ml of water (into the abdomen of small mice), and twice a week, dissolved vitamin supplements were added to the water.

2.3. Recording nestlings and fledglings

Vocalisations were recorded on a field-recording unit (Sony TC-D5 PRO II). To obtain a sound quality from wild-raised magpie nestlings that was comparable to that of the recordings of the hand-raised magpie nestlings and to observe their behaviour during the four weeks post-hatching, a few adaptations to the method had to be made. Outside, wind and other weather conditions could strongly interfere with recordings. Close proximity of the microphone to the nest was crucial to enable recording of sounds not necessarily audible at ground level. The researcher adapted an old plumber's pipe of 5 m length. The microphone was permanently taped onto the end part of the pipe and the lead from the microphone was firmly taped to the pipe to avoid wind noise and cable rattling interfering with recordings. The pipe was then roped to the strong trunk of the tree with the microphone part positioned within about a meter of the nest. The microphone was permanently switched on and every three days the entire pipe was removed after dark to replace the battery in the microphone and then reposition it. Sometimes it was also necessary to climb the tree to fit the microphone with a plastic hood to avoid damage from rain. For later recordings, when the nestlings were three weeks old or more, the microphone and stand were left freestanding near the nest on a tripod with the unidirectional microphone facing vertically upwards to the nest at a maximum recording distance of 2 m. A 30 m lead was connected to a small amplifier and a tape recording unit inside the house and remotely switched the recording unit on and off.

Hand- raised magpie nestlings and juveniles were tape-recorded in an aviary next to the author's homestead (one meter away and parallel to the house, facing the living room and desk), the inside of the house being obstructed by a number of shrubs. A microphone was hung at and taped to a main perching branch (at a height of two

meters) just 30 cm away from the nest and connected *via* a 15 m lead to the inside of the house to a Pioneer 4 track 2 channel stereo auto-reverse reel-to-reel tape deck (model RT 909) with Pioneer stereo amplifier and equipped with headphones. The uni-directional microphone for recording nestling vocalisations, wild or hand-raised, was always at a distance of no more than 2 m from the source but mostly within less than a meter away from the vocalising bird providing a crisp and clear sound and doing so at an amplitude level that permitted fine discriminations between sounds. On a separate tripod, a video camera was also fitted, the lense facing at the nest. The tape recorder was turned on at dawn and turned off at sunset and all recordings of vocalsations downloaded and dated each night. Hence, this one nest site produced an unbroken record of vocalisations while the remaining two nest-sites under observation were limited to daily sampling periods (setting up all recording equipment in the same manner as at the permanent site).

Recording of the vocalisation of hand-raised fledgling magpies largely followed the same paradigm as that used for nestlings as long as they remained in the aviary. Increasingly, however, they spent hours in the garden but volunteered to return for roosting at night in their aviary. The birds were so tame that they tended to follow the human carer around in the garden. No bird flew away and all came without being called when hungry. Recordings in such field situations were then undertaken by a mobile unit.

For free-ranging magpies, making recordings was considerably more difficult the older the magpies were because they began to range over their entire territory and increasingly separated from the family group and even from other siblings to explore the terrain on their own. In the latter case, they rarely vocalised. However, provisioning of mince-meat once a day at 10 am ensured their presence and some tape recordings.

Vocalisations were recorded daily from dawn to dusk and a total of 50 hours of nestling and fledging vocalisations were obtained from each bird. Closer analysis was limited to 9000 vocalisations over the 7 month period, as identified and tagged on the computer. Vocalisations were also tagged specifically for non-species-specific

sounds. During the recordings it had become clear that some birds were mimicking human speech within specific frequency ranges and these were tagged.

2.4. Teaching of human words

Magpies are excellent mimics of other species [66], a fact that raised the question whether magpies could be taught human speech, as one can do with most parrots. The singly-raised magpies, i.e., birds not distracted by peer contact were subjected to five-minute exposure of short human words twice a day (late morning and late afternoon) for a period of 8 consecutive weeks through the first and second month post-fledging. The words were spoken directly to the bird, not taped so as to ensure that the same person who fed the birds was also the provider of words. Feeding occurred directly after the conclusion of each teaching session and, of course, as indicated before, these were not the only feeding sessions, i.e. each speech session was at most 1.5 hrs. post the last feed. Within the five minutes of speech, the short sentences presented were interspersed with single words that formed the sentences. The vowels 'a-e-i-o-u' were present in this sample, no sample exceeded three words and each word consisted of one or a maximum of two syllables. Fricatives were avoided (dependent on the presence of lips). Words were chosen that were unlikely to be heard elsewhere or perchance. The experiment sought evidence of human words both taught and untaught.

2.5. Growth patterns

Hand-raised magpies (N-13) were weighed and measured at weekly intervals from the time of arrival to release stage. These included magpies raised for extended periods and those in shorter-term care. These measures included body weight, general body length (from shoulder to tail), leg and claw length (second digit) and the beak length and width. Body length was measured from the shoulder to the anus; beak length (exposed culmen) from the tip of the upper mandible to the top of the nares and the gape, from the edge of the beak across.

3. RESULTS AND DISCUSSION

3.1. Word learning

To report first on the 2 month experiment of teaching hand-raised magpies human words.

This experiment was entirely unsuccessful. Not one magpie ever learned a single word that was actually 'taught'. An attempt to teach words recorded on tape by the experimenter and played back to magpies also yielded no results. However, notwithstanding this failure, human sounds appeared in 2 of the magpies (but not the words that had been specifically taught) and this resulted in recording words and vowel sounds from human speech of another member of the household (not from the researcher) from whom the birds were likely to have learned the human sounds. These words were then compared with the magpies' rendering. Hence there was an unusual opportunity to compare learner and teacher, whereby the 'learner' (the birds) never appeared to be learning and had not been responsive to the teachings of the researcher and the incidental 'teacher(s)' had no idea of the impact of their voice on the birds.

3.2. Physiological development

Physical development follows similar time courses in all altricial species. Magpies undergo rapid physical development, as expressed in their growth rate, weight and overall size increase. On average, a nestling increases by 8-10 g per day for the entire nestling period (Table 1).

Beak and neck measurements were taken because both are important for sound quality, frequency range, and together with the growth of syringeal muscles, also help sound modulation and breathing control [73]. The scores for beaks from weeks 6 to older fall very much into the range of beak measures (exposed culmen) taken by Schodde and Mason (1999) [74]. They may also suggest that the sample consisted of a good mixture of males and females (sex of juveniles could not be ascertained by observation). The results demonstrate that development and lengthening of the beak not only continues after fledging but is subject to particularly rapid growth.

The results of ultimate beak length is puzzling because they showed that hand-raised magpies tended to have shorter beaks than wild-raised ones. There appears to be a natural variation of beak length of about 5 mm in this species and there is a 3-5 mm range of variation in beak length between males and females, but with a substantial overlap [74].

Table 1. Weights and measures of developing magpies.

These measures provide the whole body weight and the sizes of body and the beak, both of which are involved in sound production. Note that the adult measures refer to the beak (exposed culmen) for *Gymnorhina tibicen tibicen*, published taxonomic data by Schodde and Mason (1999) [74] and are offered here for comparison. Note the difference between male and female beak length. Data would suggest that full beak length is achieved by about the 7th week after hatching.

(As means ± variation)	Weight (in g)	Body length (in mm)	Beak length (in mm)	Beak width (in mm)
Week 2 (N = 2)	89.3 ± 40.0	51.0 ± 03.0	22.7 ± 1.0	23.7 ± 1.0
Week 3 (N = 10)	223 ±40	89.7 ±10	31.4 ±1.4	27.3 ±2.2
Week 4 (N = 12)	270.7 ±40	101.5 ±11	36.8 ±1.3	25.8 ± 1.0
Week 5 (N = 30)	306.3 ±30	102.0 ±11	39.5 ±1.5	24.4 ±1.8
Week 6 (N = 22)	355 ±25	104 ±3.0	47.6 ±4.0	21.6 ±2.0
Week 7 (N = 12)	360 ±25	106 ± 3	50.8 ±4.0	22.2 ±3.0
2 months + (N = 22)	394 ± 2.0	112 ± 8.0	52.4 ±2.0	23.2 ±2.5
Adult Measures			48-55 (m)	
			45-50 (f)	

Note that Fig. 3 indicates that full body length is reached at the time of fledging (plateaus after week 4) but weight continues to increase. At branchling stage (week 5) the growth of the beak in length slows while beak width is reduced as the soft tissue enabling gape at the corner of the beak firms up and shrinks. Beak length and width begin to diverge from 3rd week post-hatching, with length of the beak increasing.

These physical changes go hand in hand with vocal development. Fig. 4 below demonstrates the shift over a two-month period. The nestling on the left can produce a variety of sounds of varying frequency but the amplitude is not very high and many of the sounds, including the begging call (see below), sound croaky and clumsy. The bird on the right, by contrast, just two months out of the nest (12 weeks of age), has developed a full repertoire, and, according to our earlier study on song nuclei, has a fully developed song control system [32].

3.3. Begging calls in nestlings and juveniles

The results below indicate that begging calls follow two distinct periods:

a) begging calls emitted as nestlings and
b) begging calls emitted post-fledging.

Begging calls were unidentifiable as such in the first two weeks within the nest, commencing in third week. Up to the end of third week they are
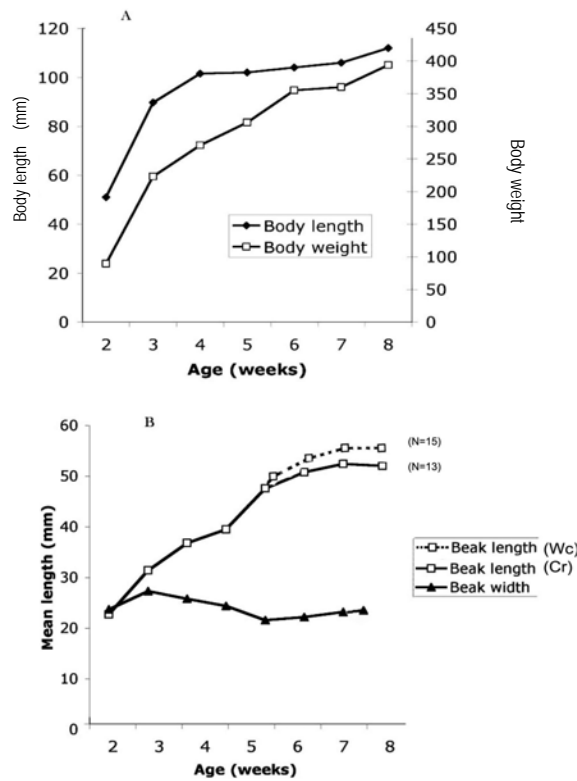
Change of body length/weight and of beak length and width by age

Fig. 3. A: Y-axis refers to mean body length and body weight in grams. **B:** depicts mean length and width of beak in mm. Data collection commenced only in the second week (no magpies were available in the first week of life). The histogram distinguishes between early parts of week 2 and 3 and late part of week 2 and 3, hence the numerals '2' and '3' appear twice on the X-axis. This indicates the rapid lengthening of the beak and the shifting ratio to the gape of the beak (width). No error bars were provided because variations among individuals were negligible (>0.2 mm). Note the dotted line above, however. Consistently, the beaks of wild-raised magpies grew a little longer and remained slightly longer.


Dramatic change in neck and beak length over 2 months

Fig. 4. Panel on the left is an image of a three-week old nestling and, on the right, a juvenile of about 12 weeks of age. The beak doubles in length and the neck length increases to almost three times the length of the nestling. These maturational changes are also reflected in the vocalisations the nestlings produce.
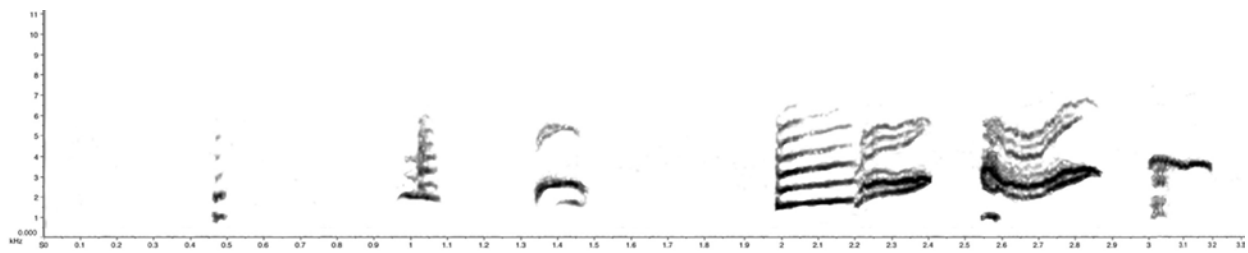
A. Begging call attempts (end of 2nd week)
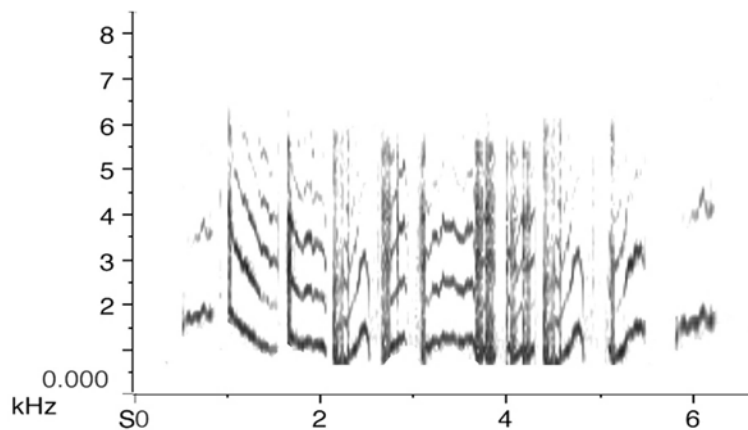
B. Unstable begging call (third week nestling)

Fig. 5. **A:** Attempts to produce begging calls in the second week post-hatching are far and few between, uncoordinated and do not yet bear the marks of a typical begging call but already have harmonics. **B:** 3-week old magpies nestling produce unstable begging sounds at about 50 dB just barely above the intensity of normal human speech, for about a total of 4 secs (X axis) first and last syllable are peeps) and with a good deal of noise/rasping sounds (greyness within each sound indicates noise). While the sounds extend to nearly 6 kHz (Y-axis), the first formant (lowest point) has moved from 4 kHz to variations between 1.5-2 kHz (the level at which most adult song is produced).

unstable in structure, very variable, of brief duration and also vary in amplitude between 40-70 dB. Fig. 5A and B are examples of entire sequences of attempted begging calls in weeks 2 and 3 post-hatching.

According to previous observations [56], adults feed nestlings consecutively and equally whether they vocalise or not. In fact, magpie parents were found to ignore begging calls by nestlings if that nestling was out of turn for feeding. The magpie may be among the few avian species to feed offspring equally and consecutively.

Shortly before fledging, the call structure takes on the characteristics and stereotypy that the call then retains (Fig. 5C). Likely reason for this change is

that fledglings are mobile and fly about in a large territory. Early post-fledging they tend not to follow the parent but the adults fly to the fledglings. Begging calls in fledglings appear to serve a dual function of contact call and begging call.

As the food-dependent offspring get older they have learned to follow the parent bird (generally from week two post-fledging onwards) [22]. After two months post-fledging, adults do so with increasing hesitation, at times even withholding food or consuming it in front of the vocalising juvenile. In these later phases, some unsuccessful begging calls degenerated into a whimper. Begging calls, a hallmark of magpie nestlings and
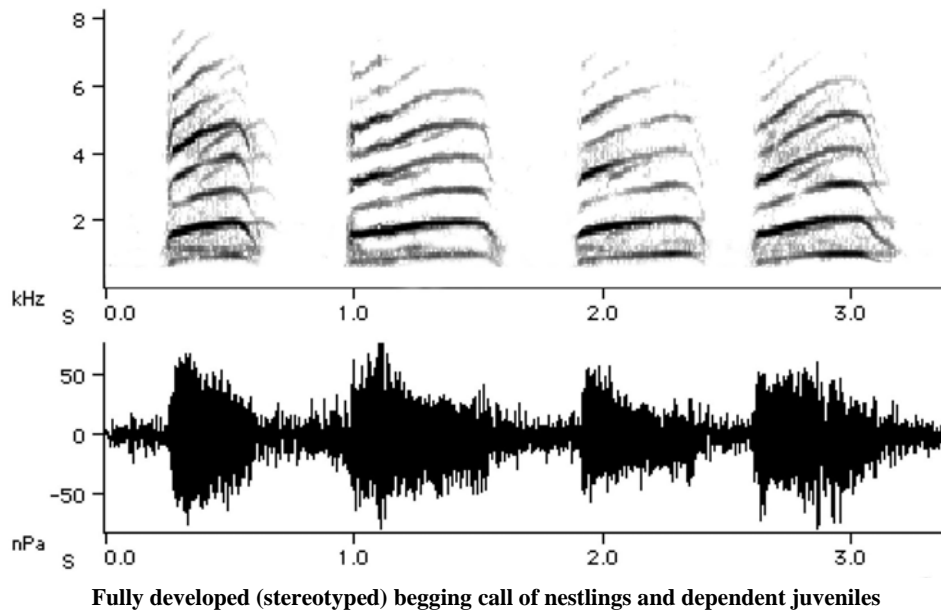
Fully developed (stereotyped) begging call of nestlings and dependent juveniles

Fig. 5C. Stereotyped powerful begging calls perfected by the last days before leaving the nest and remaining unchanged from then on, being used and emitted for the best part of another 3 months by which time parent birds begin to discourage the begging calls and the begging for food and begging behavior eventually stops. Such begging calls can be sustained for several minutes.

food-dependent juveniles, are generally not produced later in life. However, one would not call this attrition. Under certain circumstances, adults make begging calls to each other and these are the same as those vocalised by fledged juveniles.

3.4. Other vocalisations

The most common forms of vocalising of adult magpies are songs (also referred to as warble), carolling and the stereotyped generic alarm call [75] (Fig. 6). Individuals develop distinctive song and syllables in a repertoire that, within the sample, ranged from about 524 to 920 syllables with many combinatory variations. Carolling, a territorial call, consists of a series of short calls of high amplitude (80-90 kHz). Magpies use many types of alarm calls but the generic alarm call is stereotyped and rarely varies even across regions [75].

No vocalisations were recorded in the first week of life in the wild-raised magpie nestlings and no nestlings were hand-raised at this age. It is possible that faint vocalisations were present but not detectable even using a microphone just a meter away from the nest. However, by the second week, vocalisations were identified and recorded in both wild- and hand-raised groups.

The first recordings in week 2 consisted of a few irregular and very faint and high-pitched sounds (Fig. 7A). The main features of these vocalisations are the undifferentiated high-pitched peeps (at or above 4.0 kHz). These peeps occurred at intervals of 1 sec or greater (X-axis), and they occurred relatively rarely.

By the end of the second week, frequency range dropped almost to the level of adult vocalisations (around 1.5-2.2 kHz) and there is evidence of an increase in the number of harmonics. The amplitude increases markedly over the last 1.5 weeks of the nestling stage (Fig. 7B). Vocal practice consists of a combination of selective attrition and learning of novel forms [53]. New sounds/syllables were added from week three onwards but the vocalisations lacked the clear structure of adult song and continued to be very variable The melodious 'warble' or song of adults (Fig. 8) tends to be practiced post-fledging and we have shown elsewhere how juveniles deal with airflow and syringeal muscles in the practice of near pure tone sounds (absence of harmonics) that sound and flow effortless like a well-tuned wind chime [21]. It is a unique song.
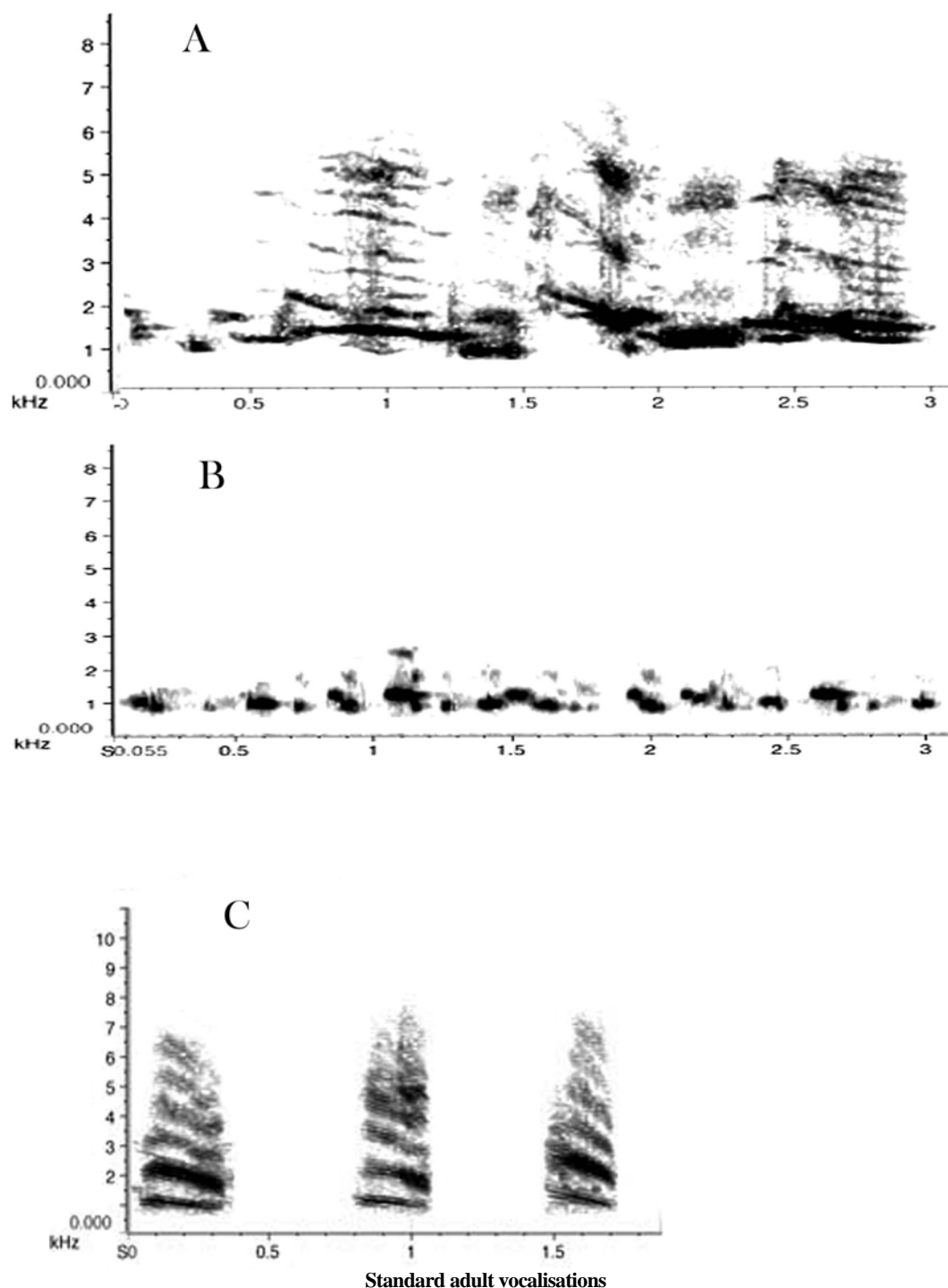
Fig. 6. X-axis: time in minutes; Y-axis: fequency in kHz. **A:** a series of loud, slurred calls called 'carolling'; a call specifically used as a terrtoral claim/announcement and also used as a joint family/group enunciation after a victory of having successfully expelled a major predator, such as an eagle. All adults join in this call which can be initiated either by an adult female or male. Juveniles are not permitted to join in. On flat terrain, the calls are audible for about a kilometer. **B:** Warble/main song of magpies, beautifully melodious, close to pure tone and can be almost continuous and maintained for hours. **C:** the stereotyped generic alarm call, by no means the only type but the one used more often than any other [75] (cf Kaplan *et al*. (2009) for elaboration on alarm calls).
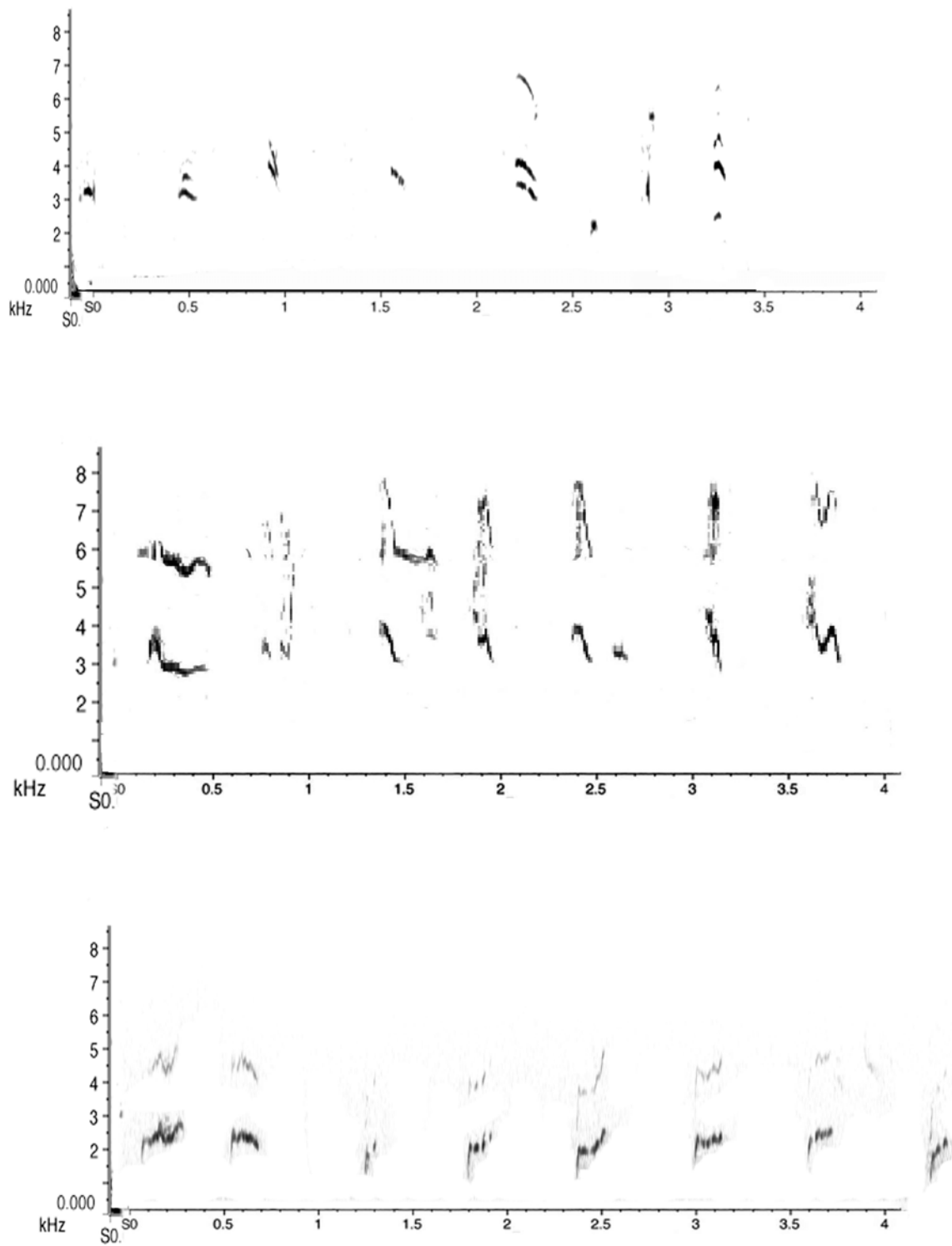
Nestling vocalisations, week 2

Fig. 7A. The range of frequency (3-7kHz) makes it eminently clear that vocalisations of magpie nestlings up to the middle of the second week post-hatching are expressed over an entirely different range of pitches than those of adults. Moreover, the acoustic structure of these calls bears little to no resemblance to adult species-specific vocalisations.
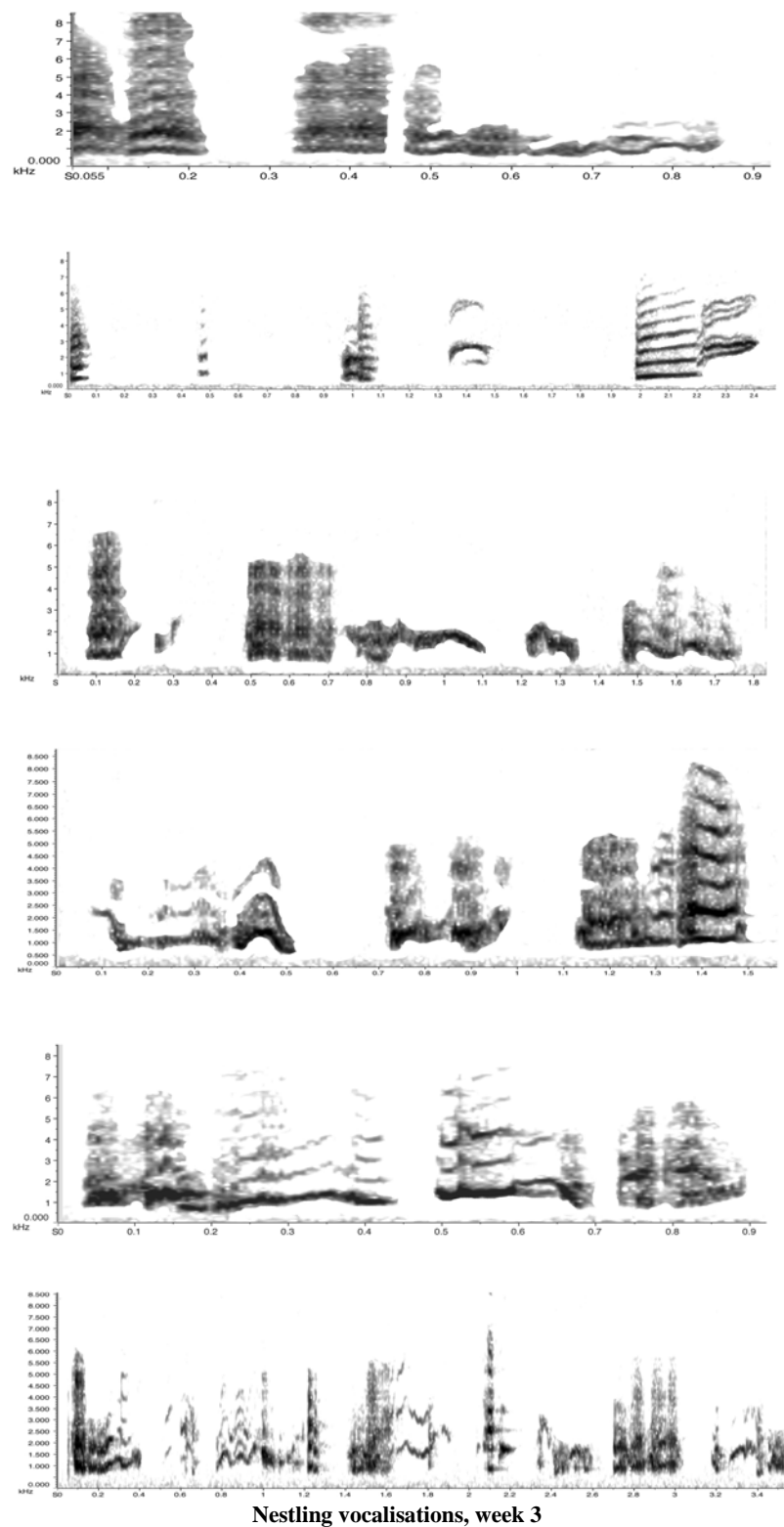
Nestling vocalisations, week 3

Fig. 7B. The species-specific warbles are very varied but the elements are already well-formed and of an energy and frequency level closer to adults. It has not been established whether some early babbling elements represent an 'overshoot' that will be abandoned by the adult, as it often happens in other songbirds.

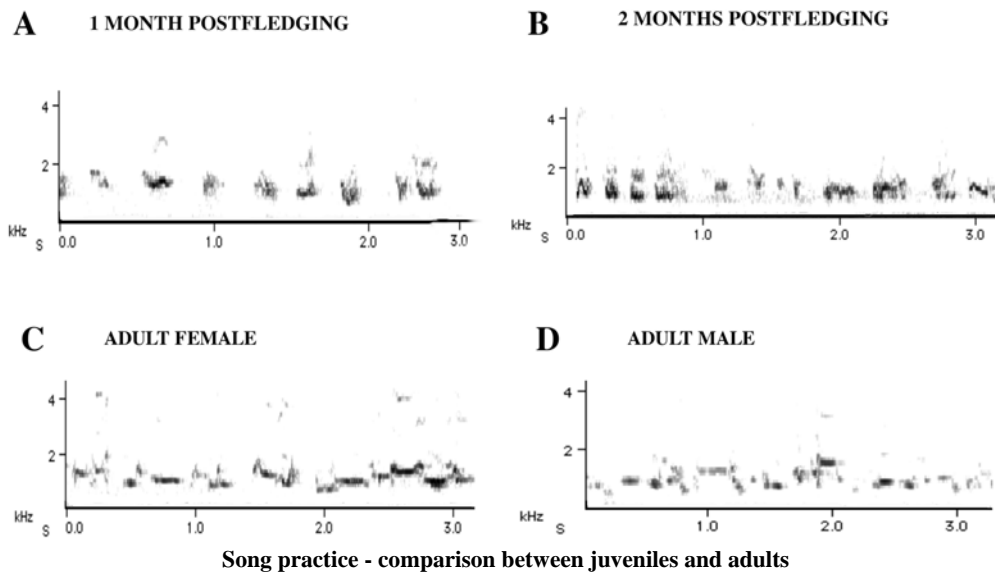**Song practice - comparison between juveniles and adults**

Fig. 8. The figure shows that the gaps between elements is relatively large even in the first month post-fledging (A) due to a need to take a breath in between, and begins to narrow by 2nd month postfledging (B) but, initially, at the cost of sound quality, sounding more rasping than melodious. Note that within 3 sec, adults produce sounds that are near continues. If broken down into elements, there are 22 for the female (C) and 20 for the male (D) while the 1st month post-fledgling manages 8 sounds in the same time, and the 2 month post fledging 12 elements. Speed of delivery, to make song sound continuous is obviously quite difficult to do for young magpies.

3.5. Summary of general developmental stages of vocalisations of free-ranging and hand-raised magpies

Each type of vocalisation appeared at a different stage in vocal development. There was little difference between hand-raised and wild-raised magpies, except that alarm calls, normally reserved for the adults, were expressed by hand-raised juveniles. Without adult supervision, it is likely that the early use of alarm calls is an artifact of a lack of appropriate socialisation into magpies' society.

Despite the care that was taken to raise the hand-raised magpies as closely as possible to the manner in which wild-raised magpies are raised, some substantial differences were found. The hand-raised juvenile magpies vocalised remarkably more often than their wild counterparts. They practised more, sang more and, in general, had a much larger repertoire than the wild magpies. Interestingly, the beak of wild magpies examined in this study seemed consistently longer than that of the hand-raised magpies but this was perhaps not conclusive and a much larger sample size would be needed.

Goldstein *et al.* (2003) [53] had developed an outline on how to recognise some basic stages of vocal development in songbirds and these seem to hold for magpies as well. These are:

1. Early vocalisation of nestlings is unstable, of low amplitude but high frequency and very undifferentiated. The findings for utterances by magpie nestlings during the second week post-hatching confirm this general observation. They are undifferentiated in terms of acoustic parameters and in terms of function. They are of extremely low amplitude but very high frequency.

2. During the latter part of the nestling period, rudimentary forms of subsong are developed and these are still distinct from adult song and consist of a combination of selective attrition and learning of novel forms.

3. In slightly later stages of vocal development (and these time frames can differ substantially between songbirds), vocalisations will include elements that will not be present in adult form, e.g. still showing high variability in structure and timing [76].

The vocal development of nestling to juvenile magpies afforded the opportunity to test whether these stages reveal something of basic principles of the way vocal learning can be achieved.

4. Social aspects of song acquisition and mimicry

Surprisingly, one of the important findings for vocal development was that parents do not sing near nestlings and nestlings ceased practicing when parents were near. Only when parents were out of sight or at least 15 m away from the foot of the tree did nestling practice resume. Distance between parent birds and nestlings seemed consistently beyond auditory range. These observations were consistent across all wild-raised groups observed. Instead of a role in facilitation of vocal learning in offspring, parent birds seemed to inhibit vocalization practice (excepting begging calls) in nestling and juvenile magpies.

These results now shed light on the lack of success of trying to teach magpies to speak, as one can teach parrots. For both those magpies the researcher clearly acted *in loco parentis*. The fact that no nestling mimicked the researcher's speech (i.e. the one who fed and cared for them) in any obvious and measurable way is consistent with the role of a surrogate parent of this species. As in the case of free-ranging magpies, the hand-reared magpies stopped any vocal practice (but often started begging) when the researcher was in visible and auditory range. It appears that vocal development in magpies may have an inbuilt mechanism that prevents vocal copying of parents, extending even to human care-givers. If offspring must not copy parent birds then the copying of words by the researcher were clearly on the taboo list.

The important point here is that vocal learning in magpies did not result from instruction because, in this species, song is not transmitted *via* the parent birds. That this inhibition is not an act of intimidation may be gleaned from the fact that both in the wild-raised magpies as well as in the captive nestlings they promptly showed begging responses as soon as the researcher walked within range of the 'nest' or parent birds appeared near the nest.

Mimicry of human speech was developed only in the specific magpies that lacked the company of their own kind and of their own age. Wildlife organisations encourage 'buddying' magpies with same-age nestlings from different clutches. Magpies are intensely social and form tight family groups and for this reason it is believed that magpies need social company to develop the behavioural skills to function successfully in such groups. While this seems a reasonable argument, the value of this approach to rearing abandoned nestlings has never been tested. That it could have effects on vocal abilities and expressions had not been considered to date.

For the two magpies in question (raised as singletons), no other same-age nestlings happened to be available, and the stunning and unexpected results strongly suggest that nestlings and juveniles learn from the ambient vocal environment.

This conclusion was reached because the only possible source of human speech sounds available to the birds were, in fact, those that carried from the living room through the open window to the aviary, situated just at a meter's distance from that window. From this distance, human speech was clearly audible. At least twice a day there were conversations at the dining room table for breakfast and dinner and often there were lunch or dinner guests at the weekend and, of course, other human speech sounds occurred in the house and occasionally outside. Inevitably, the conclusion has to be drawn that sounds (including words and phrases) were acquired especially from the round table conversations and discussions of householders and visitors, none of whom were caregivers.

Why they acquired human speech intonation and words is far harder to answer and at this point would be too speculative. Clearly the caregiver was a significant element in the magpies' lives and the vocalizations that the surrogate parent produced became part of their soundscape experience.

This also raises the possibility that nestlings listen to and acquire vocalisations of magpie neighbours. It is known that adult magpies, when they finally manage to acquire their own territory (usually not before the age of 5) are known to begin

overlapping with neighbour's songs. A study by Farabaugh *et al.* (1988) [72] found that the percentage of overlap among permanent territorial neighbours can be as high as 25 percent. Perhaps magpies begin eavesdropping on neighbours while still in the nest and partly get their impetus for learning and vocal practice from other conspecifics within or even outside their natal territory. As shown elsewhere [77], however, magpie singing (not including alarm calls and similarly short calls) drops dramatically before and during the breeding season and such vocalisations are usually uttered by non-breeding magpies. Of course, one could argue that song is genetically endowed and merely requires practice to express itself fully. It does not explain the mimicry, however, which is clearly not a species-specific utterance and therefore requires learning.

4.1. Mimicry development, learning and retention as evidence for brain plasticity

A major result of the project was the discovery of vocal mimicry in the singleton magpies, held from late nestling stage to early adulthood (3.5 weeks to 1.2 years; 2 weeks to 7 months). As will be shown below, they developed sustained mimicry of human speech intonation, words and phrases, but, crucially, not the words that the experimenter had tried to teach.

Now that the typical sounds and developmental stages of magpie vocalizations have been mapped out in this paper, the mimicry can be placed into this developmental time-frame and it can also be shown in sonograms that such mimicry is different in some crucial ways.

Mimicry of the human voice was not just something that happened and occurred from one minute to the next. We know of even relatively mimicry-poor bird species (songbirds as well as parrots) that they can spontaneously give a recognizable rendition of 'Hello' (usually said with an 'a' rather than an open 'e' sound). Clearly, there is little one could say in terms of speech development. However, in the magpies it was possible to trace the development of speech mimicry and this is one rare case in which babbling in human language development can be directly compared with that of a songbird's babbling of human language.

The earliest stage might not even be termed mimicry because it presents no single identifiable words (Fig. 9), and yet, without a doubt, it contained phonation that was entirely different to all the vocalizations that had been so carefully documented in the magpie's vocal development. It had an internal consistency (more harmonics, higher energy input, sustained amplitude and specific emphases) that made the sequences sound like human sentences.
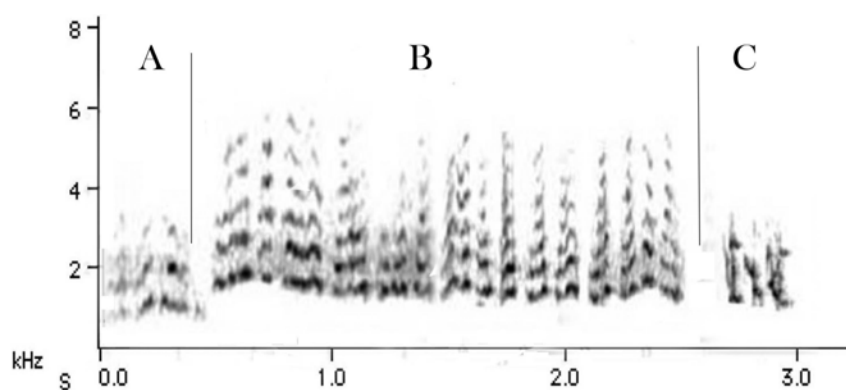
Prelinguistic utterances of human speech sounds by a magpie

Fig. 9. The vertical bars separate different sound features. Segment **A** shows species-specific vocalisations; **B:** babbling sequences mimicking human speech intonation; **C:** returning to its own vocalisations - this particular phrase is an individual signature with which this particular bird ended most of its song sequences. (A sound file of this segment can be made available by the author on request by e-mail).

Interestingly, Stager and Werker (1997) [78] had discovered that in early vocal developments, human infants listen for more phonetic detail in speech perception than for word-learning tasks. It would seem that the same might apply to magpies and, given that they are not tutored, the importance of selective listening for phonetic detail may be crucial.

In the next phase of this mimicry of human sounds, vowels appeared during the babbling.

Vowel 'a' (as in 'ball') was voiced first and often in combination with a consonant that could be taken for a 'w' or a 'b' so that these could be grouped into syllables and repeated and become strings of 'baw-baw-baw' (Fig. 10, Panel 1). Within days, this was followed by open 'o' sounds as in 'woe', a sound that could also be changed to a closed 'o' as in motor.

In the third phase, the birds began to make up new combinations. One of the favourite combinations
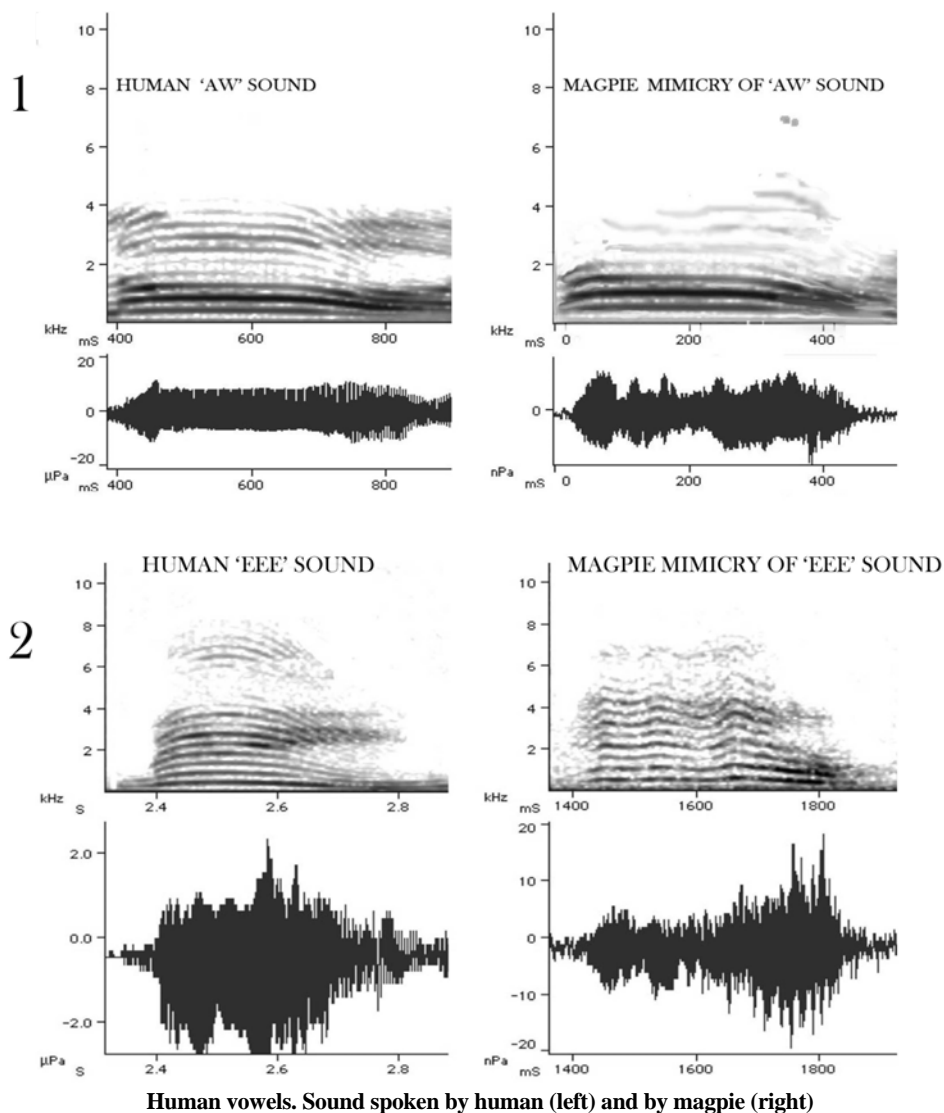

Human vowels. Sound spoken by human (left) and by magpie (right)

Fig. 10. Vowel sounds. Panel 1: The 'aw' sound produced by a human speaker (left) and a magpie (right). The first formant is identical (and lower than magpie produces in its own song). Note the similarity also in the pressure (waveform). Panel 2: the 'eee' sound is mimicked; the unsteady lines indicate that the bird had some difficulties keeping the sound steady, Both 'aw' and 'eee' are nevertheless clearly recognisable as human speech vowels.
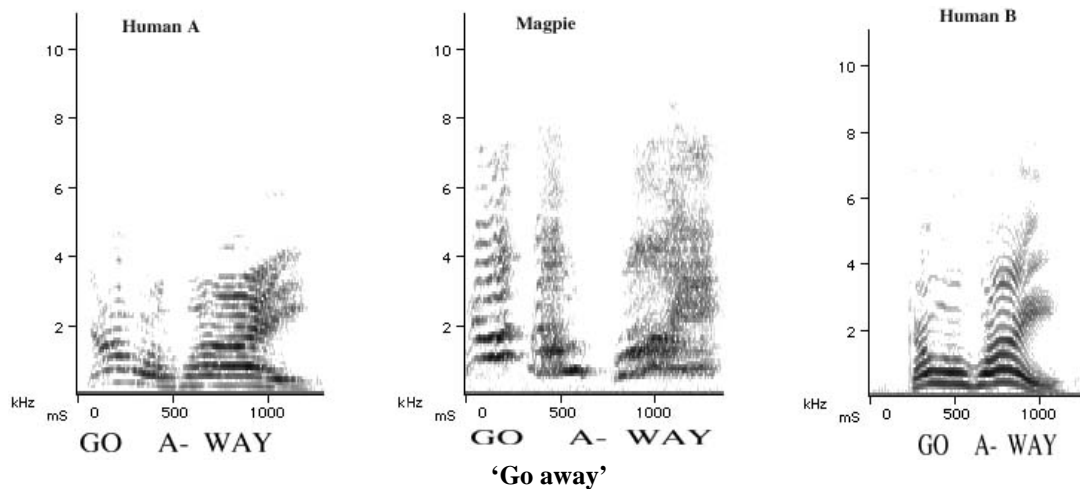
Fig. 11. Fully formed mimicked words were tested against 2 adult human pronunciations of the same words. The magpie applied much higher amplitude to words than normal speech sound- the last section 'way' was positively souted and hence carries a good deal of noise. It seems that the birds needed to raise the volume in order to reproduce the sounds. The words are very clear (Supplementary sound file can be made available by the author on request by e-mail).

of Bird A was the combination 'ko-yuk' with rising tone, sometimes repeated two to three times in the one phrase. It appeared that the bird found the darker and more closed sounds (a sound as in 'low' rather than the open 'lord') easier to produce. The 'yook' segment sounded like a closed 'u' as in 'look'.

The 'e' sound (as in 'cheer') developed last (after two months from the first onset of mimicked sounds) (Fig. 10, Panel 2). The 'i' as in 'mimic' was the least popular but sometimes strewn into the 'kuyuk' syllables to become 'kiyuk'. Finally, expressive 'oh's and 'ahs' appeared and then followed by actual words and phrases. The most dominant ones were 'Go away', and "I have got dinner for you".

Another major finding of this research project has been the discovery that magpies, when acquiring human speech, unaided, have stages of babbling in a manner nearly identical to the babbling stage of human infants (Figs. 11, 12). This discovery was possible only because of the methodology employed (i.e. recording all vocalisations throughout the entire period of development) and resisting the temptation to merely sample their vocalisations in shorter periods. It is also likely that the early stages of these vocal developments could have been missed entirely (as meaningless snippets within general species-specific vocal practice),

had it not been possible to trace back the words and sentences to some phonetic beginnings and hence establish a pattern.

The findings of human intonations, of mimicry of syllables and words in magpies may be summarised as follows:

1. Before the acquisition of human words, a magpie is engaged in a pre-mimicry stage consisting of babbling that mimicked the general sound of speech but contained no recognizable words (as shown in Fig. 9 above)

2. When an element of this babbling was amplified, it was found to have many of the characteristics of human vowel sounds, such as close harmonics, broadband and the first formants under 1 kHz.

3. Consonant-vowel combinations were the rule rather than the exception in the magpie babbles, very similar to the way human infant babbling develops as will be outlined below.

4.2. Babbling in infants

Babbling in human infants is the period of vocalization expressed between vegetative/crying sounds on one hand and first words on the other and is located in a period between 2-10 months of age [79]. There are now several recognised stages in infant babbling in the first year of life
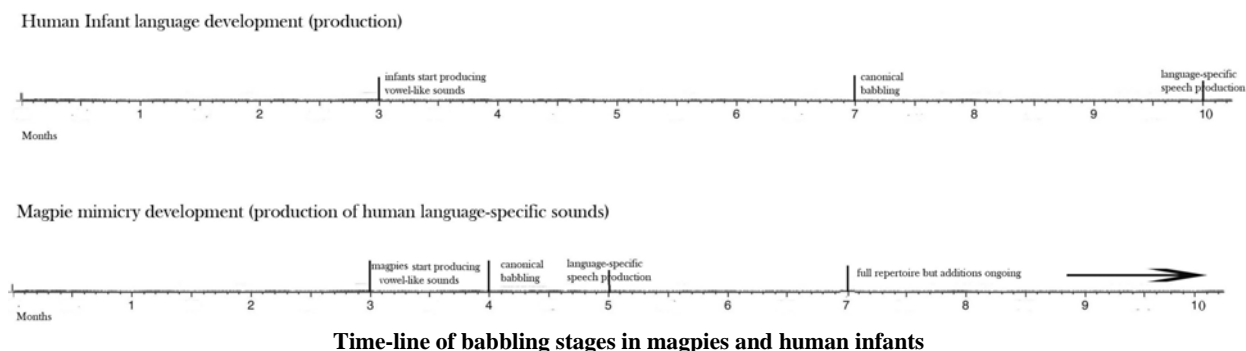
Human Infant language development (production)

Magpie mimicry development (production of human language-specific sounds)

Time-line of babbling stages in magpies and human infants

Fig. 12. Principally, there are similar stages of babbling development but they happen over a shorter time-span in magpies suggesting that there appear to be similar rules at play in vocal learning, regardless of evolutionary distance of species.

[80]. In the phonation stage, from birth to 2 months of age, infants gradually become more able to manipulate normal phonation in production of quasi vowels. From 1 to 4 months of age, infants gradually become more capable of manipulating their vocal tract during voicing in production of "cooing" and "gooing" sounds [81]. In the expansion stage, from 3 to 8 months of age, infants gradually become more able to produce full vowels and marginal babbles [82].

Early babbling vocalizations are composed of simple and unstructured sounds, but within several months one can identify vocal elements that are clearly derived from the native language, and those structured sounds then further evolve into words [83]. In summary, the babbling stage in magpies followed the same or at least similar trajectory as found in human infants (Fig. 12), including stages of consonant-vowel (CV) combinations that MacNealage and Davis (2000) [84] found in human infants, consisting of 'a' and 'o' sounds. Moreover, one bird remained in this babbling stage for an entire month (the other just under a month) before the first actual mimicry of speech appeared but, in that time, quickly developed other vowel and consonant combinations. The process took from the 3rd month until, at the beginning of the 5th month post-hatching, fully formed human phrases appeared.

MacNeilage and Davis (2000) [84] identified three sequences of sound patterns common to babbling in humans in general and two combinations were found to be common to several languages tested. Theoretically, this opens the door to the hypothesis

that basic phonetic developments may be universal in humans. These combinations are consonant-vowel (CV) combinations and the three combinations found consistently in several languages were 'mama, dada and gogo', sounding an 'a' as in 'bath' and an 'o' as in 'dog'.

The claim made is that CV combinations form the basis for the lexicon and that such phonation, independent of needs and distress (such as crying, growling) and non-cry sounds during the second to the fourth month, lays the foundation for later speech patterns. This is believed to be so partly because such phonation is always egressive as is normal speech. Linguists and early childhood development scholars usually distinguish between two major types of babbling, a repetitive type (also called reduplicated), and a variegated type [82, 84]. The latter refers to changes either in consonant or vowel. These two stages appear to occur successively [79]. Crucially, development of vocal utterances follows a number of stages and some of these are circumscribed by sensori-motor development while others are constrained by perceptual and social (shaping of response) factors.

4.3. Speech acquisition phases in birds and humans

There is now a growing literature comparing the vocal development of human infants and the development of birdsong because some important similarities between vocal acquisition in birds and humans have been noted. One of them concerns the importance of auditory feedback as a crucial

precondition to song learning or, rather, the feedback mechanisms that are now regarded as a crucial element for song learning. Moreover, such learning may be confined to a critical period in human infants [31, 53, 85, 86]. Severe hearing-impaired infants, for instance, show a significantly delayed onset of babbling and any of their vocal productions show a restricted formant frequency range. Also, their sounds are of longer duration and have a limited phonetic and syllabic inventory compared to infants of normal hearing [87, 88]. It is not known whether this pertains to babbling and song development in birds although we know that deprivation of auditory feedback prevents normal song development in birds, as said before. 'Babbling', a repertoire of sounds that increases at a rapid rate from the third week post-hatching, may thus have an important role in the development of adult vocalisations. The magpie's development of babbling and speech also followed a similar sequence of stages, as represented in Fig. 12. Results show that any combinatory babbling (such as baba) was preceded by a series of vocalisations that consisted entirely of syllables that had identified the intonation of human speech.

In summary, the babbling stage in magpies principally followed the same or at least a similar trajectory as found in human infants (Fig. 13), including stages of consonant-vowel (CV) combinations in human infants, starting with 'a' and 'o' vowels [84]. Moreover, one bird remained in this babbling stage for an entire month (the other just under a month) before the first actual mimicry of speech appeared but, in that time, quickly developed other vowel and consonant combinations. The process took from the 3rd month until, at the beginning of the 5th month post-hatching, fully formed human phrases appeared. Magpies, when acquiring human speech unaided, thus have process of sound acquisition a manner nearly identical to the babbling stage of human infants (Fig. 12). This discovery was possible only because of the methodology employed (i.e. recording all vocalisations throughout the entire period of development) and resisting the temptation to merely sample their vocalisations in shorter periods.
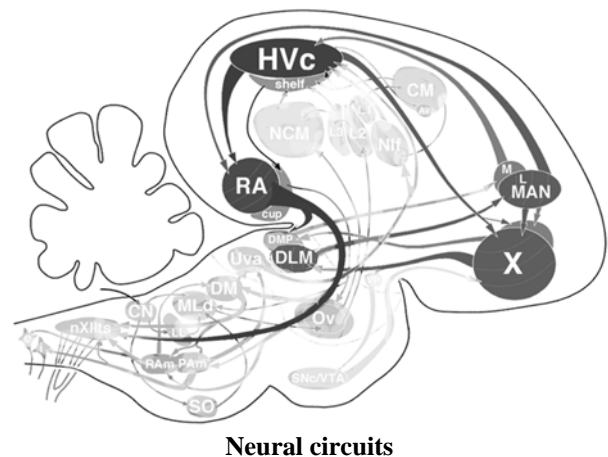

Neural circuits

Fig. 13. We now know a great deal about the dynamics of song perception and reproduction. However, increasingly developmental data suggest that not all of the essential circuits are equally present or needed at certain stages of development. In magpies, the link between HVC and area X (marked x) seems to be entirely missing, while in the vocal development of the zebra finch the HVC appears not to be involved.

4.4. Neural connections and song

Almost 20 years ago Doupe and Kuhl (1999) [31] outlined common themes and mechanisms in birdsong and human speech. Since then quite a number of sophisticated papers have identified such mechanisms by looking in detail at the human and the bird brain. Aronov and colleagues [89, 90] found that different forebrain circuits may be involved at different stages of vocal development in songbirds. By 2014, Tchernichovski and Marcus [83] argued that the capacity to flexibly assemble vocal sounds develops in a similar, stepwise manner across species. Therefore, universal features of vocal learning go well beyond the capacity to imitate and tell us something fundamental in sound acquisition across species.

It was shown before that the song system of song birds is completely mapped out and, more than that, we understand the dynamics of sound input and output, taking certain routes across the forebrain (Fig. 13). But there is now increasing evidence that certain parts of the circuit once considered an integral part of the song system, may either not be needed or may have different roles at different stages of vocal development.

Among others, the present study raises the question whether crystallised song or open song learning requires activation of different pathways in the brain at certain stages of development. And what precisely the involvement of certain nuclei is in songbirds that are open learners, may improvise and mimic. Roberts *et al*. (2012) [91] have shown that song nucleus HVC (high vocal center) is involved in the acquisition of song template with direct involvement of the sensory-motor system in the very initial stage of acquiring a memory template for vocal learning. The present results also raise the question whether neural networks are aligned differently between open learners and songbirds producing crystallised song. Then there is a further problem that Area X for instance seems to be crucial in song learning. Disruptions of area X and LMAN is (lateral magnocellular nucleus of the nidopallium) during tutoring prevent the development of an accurate copy of the tutor's song, as London and Clayton (2008) [92] found. Clearly, there is a good deal more to learn how accurate copying of mimicked sequences occurs and why area X is disrupted.

Importantly, Aronov *et al*. (2008) [89] discovered that babbling/subsong in zebra finches bypasses the HVC (high vocal center), and at the early stages of vocal development, the expression of zebra finch subsong require LMAN (lateral magnocellular nucleus of the nidopallium), a forebrain nucleus involved in learning but one not needed in adult singing. Thus song learning has a separate circuit from that used in adult song.

We studied the song system in juvenile and adult magpies of both sexes and the nucleus of area X was clearly identified [32]. Intriguingly, magpies differ from other songbirds in that there is no projection from HVC to area X. If confirmed in a larger sample one day, this is particularly pertinent because the HVC to area X connection is thought to be very important in song learning (see Fig. 13 above). This may suggest a possible and perhaps even crucial difference between magpies and other songbirds studied so far and would require more research.

5. CONCLUSION

A number of species of songbirds undergo a protracted period of sensory-motor development at which time they progress from plastic subsong to highly crystallized stereotyped song of the adult [73]. However, model species used over many decades in research to understand these mechanisms of vocal production and acquisition tend to have some characteristics that cannot necessarily inform the present study.

Equally, the stages of development of subsong and full song have been most fully appraised in species in which the male develops song as part of a reproductive strategy. His song may be shaped by the females for whom males compete. Female zebra finches chose their mates by choosing the male with the 'best' song. Female zebra finches will actively pick out males with long repertoires, and higher frequencies [93]. This has known physiological consequences as males with a larger HVC sing larger repertoires [94]. Female canaries show mate selection similar to the zebra finch, as they too choose mates on song repertoire size and complexity [95]. Alternatively, young males may learn skills from a successfully breeding male, and these skills may include learning song [96] or how to build a bower [97] they are defined and circumscribed by the very specific function they need to fulfil in breeding seasons.

In some unusual cases, as in parasitising cowbirds, *Molothrus ater*, young males do not have an opportunity to learn their own song from a male tutor (their host parents have entirely different vocalisations) but their song is shaped by females during the breeding season by responding more strongly to specific types of vocalisations but not to others [98]. Hence, a time-table for subsong and full song practice in these species includes learning but not producing all that has been learned in one season, attrition of elements and crystallization of song during the subsequent breeding season [76, 99].

Yet crystallised song may not be entirely fixed. Roy and Mooney (2007) [100] have shown that even stable, crystallised song can change its pattern, a process known as decrystallization. New syllables, phrases, indeed, new repertoires, may be produced in each successive season (as is the case in nightingales and canaries) and these may have been acquired *via* a process of improvisation, rather than by rote learning from a

tutor, or they may be determined by females, who may prefer certain elements over others. For instance, canary females respond to higher trill rates in males with higher rates of solicitation displays and thus they shape the song of adult males [101]. Yet a timetable is, nevertheless, present and it is determined by the breeding season. In magpies, song is not tied to the breeding season as has been shown before.

This study has taken as its model an accomplished songbird that has no fixed end-point for song development, whose song was shown to develop without the direct input (tutoring) by parent birds. It has produced the first comprehensive account of vocal development and of babbling in a songbird. In tracing this development, a number of important cross-links have been established to physical development on one hand and social development on the other. Vocal learning was demonstrated by the emergence of mimicry, showing not only that learning occurred but also that vocal practice improved the initial mimicry, reconfirming the discovery by Prather and colleagues (2008) [49] of the presence of mirror neurons. Interestingly, the study has also shown that song/mimicry learning is indeed a social process, as Beecher (2016) [102] showed in song sparrows, *Melospiza melodia* even if the outcome is procured by eavesdropping of sounds (here human speech). In the study by Beecher it was concluded that social interaction appears to be critical in song learning, but indirect effects (eavesdropping on adults) seem to be at least as important as direct interaction between the young bird and his tutor-neighbours. In the case of the magpies, only those that were raised singly developed very detailed and competent mimicry of human speech, suggesting that the social link to a human carer had an impact as to what was learned.

Babbling in infants has been equally perplexing and has occupied researchers for many decades. Those who have argued for a maturational approach have attributed rather little weight to this stage of vocal development, even of repetitive babbling, and regarded this as a side-product of maturation and of no significance in speech development. Yet there is evidence, at times termed 'babbling drift', showing that babbling sounds increasingly resemble sounds of early speech. Learning theory, on the other hand, recognised that the initial amorphous form of sounds is gradually shaped into the right intonation and speech-appropriate babbling. However, there are also sounds produced during babbling that are often not reproduced in early speech.

These theories have been discussed for decades now but, as in infant babbling, the babbling by magpies is also not entirely explained by either model. A cognitive model which by now also has a history spanning several decades argues rather that babbling is a form of socially significant knowledge acquisition [103] and such acquisition seems to occur in specific and logical steps, from an amorphous beginning in which the intonation of the mother tongue of the infant is reproduced (but without syllables), as was also the case in magpie rendition of human speech, progressing to repetitive babbling in which simple sound units (such as bababa) are repeated, followed by more complex vowels and consonant pairs which eventually begin to sound like words.

Even the cognitive theory might not quite explain the actual process of the acquisition of speech patterns in infants and magpies alike. Importantly, as Oller had noticed as early as 1980 [82], no matter what the linguistic environment, infant babbling proceeds in the same manner and stages of babbling across cultures and languages. The universality of core elements in the process of trying to approximate speech, suggests strongly that there must be sensori-motor constraints on how language acquisition can be achieved. More exciting is the suggestion here that such constraints and organisational patterns seem to apply also to birds, such as magpies used in this study. Not only were the stages (while in shorter time span) the same as in infants, even the development of vowels and the order in which they appeared ('a' first followed by 'o', for instance) hints at universal principles associated with vocal learning, at least in species with similar brain plasticity over a lifetime.

Motivational questions for learning human sounds have not been considered here because this would be highly speculative. The nestlings and juveniles are exposed to an ambient auditory environment and the responses depended also on perception, discrimination, and sensitivity to acoustic properties of speech in humans and animals [64].

Memory plays a role in song learning generally, of course, but reinforcement through social encounters, and motivational factors may add important dimensions for learning and retention. We do not know what these might be in the case of mimicry, say, compared to a breeding song. The present study was able to demonstrate how mimicry was acquired, retained and improved and thus able to show the degree of plasticity of learning and how learning and memorising in this context might have taken place.

It has provided the first evidence of identical progression of babbling in birds as in humans. Human speech sounds were identified in birds and these were then traced and compared with the babbling stages in human infants. Analysis of the babbling samples suggests that learning of vocalisations may be rule-governed by similar principles as babbling in humans. Sceptics could argue that this specific case was an artefact and can tell us nothing because human speech is not a natural part of a songbird's vocabulary. This is certainly true but one might counteract that much information was derived from teaching great apes American sign language in order to uncover some principles about memory, prelinguistic and symbolic understanding *via* means far removed from the natural context of primate communication. Researchers were successful in extracting information that would likely never have surfaced without this technique.

It is also clear that we believe mimicry in birds to be largely a process of imitation as an endpoint, not as a process for further development and transition into language or into what Piaget had called 'deferred' imitation referencing intentionality and memory [104]. This is not entirely true as argued elsewhere [105]. Suffice it to say here that there may be convergences that are both enabling as well as constraining so that certain brain developments become rule-governed.

In zebra finches, song was learned from a tutor on a one-to-one basis. By contrast, this paper reports the discovery that an open learner like the Australian magpie never copies a parent bird but will acquire syllables and phrases from the social group. It would be a matter of further research whether young magpies in their natal territory also integrate syllables or phrases from neighbouring groups. It is certainly known that adult magpies share about 25% of their song repertoire with neighbours [70].

It remains to be seen as to whether song development in birds with crystallising song differs in some crucial ways in their neuronal connectivity from open learners, and whether open learners have a type of neuronal connectivity, dynamics and memory system that is closer to that of humans of similar life-long brain plasticity, as this paper might well suggest.

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CONFLICT OF INTEREST STATEMENT

None.

REFERENCES

1.   Kaplan, G. 2006, Australian Magpie Voice: HANZAB, vol.7(A), J. Peter (Ed.), OUP, 605-608, 613-616.
2.   Kaplan, G. 2008, The Neuroscience of Birdsong, P. Zeigler and P. Marler (Eds.), Cambridge University Press, 153-170.
3.   Marler, P. 1970, J. Comp. Phys. Psych., 71, 1-25.
4.   Kuhl, P. K. 2003, Proc. Natl. Acad. Sci., USA, 100, 9645-9646.
5.   Tchernichovski, O. and Marcus, G. 2014, Curr. Opinion in Neurobiol., 28, 42-47.
6.   Soha, J. A. and Peters, S. 2015, Ethol., 12, 933-945.
7.   Janik, V. M. 2014, Curr. Opinion in Neurobiol., 31, 28, 60-65.
8.   Sanvito, S., Galimberti, F. and Miller, E. H. 2007, Ethol., 113(2), 137-146.
9.   Poole, J. H., Tyack, P. L., Stoeger-Horwath, A. S. and Watwood, S. 2005, Nature, 24, 434(7032), 455-6.

10. Stoeger, A. S., Mietchen, D., Oh, S., de Silva, S., Herbst, C. T., Kwon, S. and Fitch, W. T. 2012, Curr. Biol., 22(22), 2144-8.

11. Pettigrew, J. D. 1986, Science, 231, 1304-1306.

12. Baptista, L. F. and Schuchmann, K. L. 1990, Ethol., 84, 15-20.

13. Gahr, M. 2000, J. Comp. Neurol., 426, 182-196.

14. Gramza, A. F. 1970, Z. für Tierpsych., 27, 971-983.

15. Pepperberg, I. M. 1981, Z. für Tierpsych., 55, 139-160.

16. Farabaugh, S. M., Linzenbold, A. and Dooling, R. J. 1994, J. Comp. Psych., 108, 81-92.

17. Sibley, C. G. and Ahlquist, J. E. 1990, Phylogeny and Classification of Birds, Yale University Press, New Haven, CT.

18. Jarvis, E. D. 2004, Behavioral Neurobiology of Birdsong, H. P. Zeigler and P. Marler (Eds.), Annals of the NY Acad. of Sc., 1016, 749-777.

19. Güntürkün, O. and Bugnyar, T. 2016, Trends in Cogn. Sc., 20(4), 291-303.

20. Marler, P. 1991, Trends in Neurosc., 14, 199-206.

21. Suthers, R., Wild, M. and Kaplan, G. 2011, J. Comp. Physiol., A, 197(1), 45-59.

22. Kaplan, G. 2017, Symmetry, 9(7), 99.

23. Wright, T. F., Hara, E., Young, A. M., Araya, S. M., Dahlin, C. R., Whitney, O., Lucero, E. and Smith Vidaurre, G. 2015, J. Acoust. Soc. of America, 138(3), 1880.

24. Konishi, M. and Akutagawa, E. 1985, Nature, 315, 145-47.

25. Vicario, D. S. and Yohay, K. H. 1993, J. Neurobiol., 24, 488-505.

26. Gobes, S. M., Jennings, R. B. and Maeda, R. K. 2017, Behav. Processes, In Press.

27. Nottebohm, F. 1977, Lateralization in the Nervous System, S. Harnard (Ed.), Acad. Press, New York, 23-44.

28. Mundinger, P. C. and Lahti, D. C. 2014, Proc. R. Soc. B, 281(1781), 20132631.

29. Nowicki, S., Peters, S., Searcy, W. A. and Clayton, C. 1998, Animal Beh., 57, 1257-64.

30. Nelson, D. A. and Poesel, A. 2014, Behav. Ecol. Sociob., 68(11), 1741-52.

31. Doupe, A. J. and Kuhl, P. K. 1999, Annu. Rev. Neurosci., 22, 567-631.

32. Deng, C., Kaplan, G. and Rogers, L. J. 2001, Behav. Brain Res., 123(1), 89-102.

33. Rose, G. J., Goller, F., Gritton, H. J., Plamondon, S. L., Baugh, A. T. and Cooper, B. G. 2004, Nature, 432,7538.

34. Nottebohm, F., Alvarez-Buylla, A., Cynx, J., Kirn, J., Ling, C-Y, Nottebohm, M., Sutter, R., Tolles, A. and Williams, H. 1990, Proc. Natl. Acad. Sci., USA, 329, 115-24.

35. Kroodsma, D. E. and Pickert, R. 1984, Animal Beh., 32, 395-399.

36. Braaten, R. F. and Reynolds, K. 1999, Animal Beh., 58, 105-111.

37. Gobes, S. M. and Bolhuis, J. J. 2007, Curr. Biol., 17, 789-793.

38. Galef, B. G. Jr. 1998, Advances in Psychological Science, 2, Biological and Cognitive Aspects, M. Sabourin, F. Craik and M. Robert (Eds.), Psychology Press, 275-299.

39. Clayton, N. S. 1987, Animal Behav., 35, 714-721.

40. Zann, R. 1990, Animal Behav., 40, 811-828.

41. Baptista, L. F. and Gaunt, S. L. L. 1997, Social Influences on Vocal Development, C. T. Snowdon and M. Hausberger (Eds.), Cambridge University Press, 23-40.

42. Adret, P. 1993, Animal Behav., 46,149-159.

43. Hultsch, H., Schleuss, F. and Todt, D. 1999, Animal Behav., 58, 143-150,

44. Baylis, J. R. 1982, Acoustic Communication in Birds, D. Kroodsma and E. H. Miller (Eds.), Academic Press.

45. Goodale, E., Ratnayake, C. P. and Kotagama, S. W. 2014, Ethol., 120(3), 266-274.

46. Igic, B., McLachlan, J., Lehtinen, I. and Magrath, R. D. 2015, Proc. R. Soc. B, 282(1809), 20150798.

47. Goodale, E. and Kotagama, S. W. 2006, Proc. R. Soc. B, 273(1588), 875-880.

48. Dalziell, A. H., Welbergen, J. A., Igic, B. and Magrath, R. D. 2015, Biol. Rev., 90 (2), 643-668.

49. Prather, J. F., Peters, S., Nowicki, S. and Mooney, R. 2008, Nature, 451(7176), 305-310.

50. Tchernichovski, O. and Wallman, J. 2008, Nature, 451(7176), 249-250.

51. Kroodsma, D. E., Vielliard, J. M. E. and Stiles, F. G. 1996, Ecology and Evolution of Acoustic Communication in Birds, D. E. Kroodsma and E. H. Miller (Eds.), Cornell UP, Ithaca & London, 269-281.

52. Baptista, L. F. and Petrinovich, L. 1986, Animal Behav., 34(5), 1359-1371.

53. Goldstein, M. H., King, A. P. and West, M. J. 2003, Proc. Natl. Acad. Sci., USA, 100, 8030-8035.

54. de Boysson-Bardies, B., Sagart, L. and Durand, C. 1984, J. Child Lang., 11(1), 1-15.

55. Catchpole, C. K. and Slater, P. J. B. 2008, Bird Song: Biological Themes and Variations, Cambridge University Press, Cambridge.

56. Kaplan, G. 2008, The Australian Magpie: Biology and Behaviour of an Unusual Songbird, CSIRO Publishers, Melbourne.

57. Dowsett-Lemaire, F. 1979, Ibis, 121, 453-468.

58. West, M. and King, A. P. 1990, Am. Scient., 78, 106-113.

59. Hausberger, M., Jenkins, P. F. and Keene, J. 1991, Behaviour, 117(1), 53-81.

60. Chisholm, A. H. 1948, Bird Wonders of Australia, Angus and Robertson, Sydney.

61. Moore, B. R. 1996, Social Learning in Animals, The Roots of Culture, C. M. Heyes and B. G. Galef, Jr. (Eds.), Academic Press, New York, 245-265.

62. Kelley, L. A. and Healy, S. D. 2011, Curr. Biol., 21(1), R9-R10.

63. Greenlaw, J. S., Shackelford, C. E. and Brown, R. E. 1998, The Wilson Bull., 110, 431-434.

64. ten Cate, C. 2014, Curr. Opin. Neurobiol., 28, 157-164. doi: 10.1016/j.conb.2014.07.019

65. Tyack, P. L. 2016, Vertebrate Sound Production and Acoustic Communication, Springer Int. Publishing, 261-295.

66. Kaplan, G. 2000, Int. J. Comp. Psych., 12(4), 219-241.

67. Collins, J. 1983, Geelong Naturalist, 20, 80.

68. Sanderson, K. and Crouche, H. 1993, Austral. Bird Watcher, 15(4), 162-164.

69. Chisholm, A. H. 1937, Ibis, 1, 703-721.

70. Brown, E. D., Farabaugh, S. M. and Veltman, C. J. 1988, Behaviour, 104(1-2), 1-28.

71. Brown, E. D. and Farabaugh, S. M. 1991, Behaviour, 118(3-4), 244-274.

72. Farabaugh, S. M., Brown, E. D. and Veltman, C. 1988, Behaviour, 104, 105-125.

73. Podos, J., Sherer, J. K., Peters, S. and Nowicki, S. 1995, Animal Behav., 50, 1287-1296.

74. Schodde, R. and Mason, I. J. 1999, The Directory of Australian Birds, Passerines, CSIRO Publishing, Melbourne, Vic.

75. Kaplan, G., Johnson, G., Koboroff, A. and Rogers, L. J. 2009, Open Ornithol. J., 2, 7-16.

76. Marler, P. and Peters, S. 1982, Dev. Psychobiol., 15, 369-378.

77. Kaplan, G. 2008, The Neuroscience of Birdsong, P. Zeigler and P. Marler (Eds.), Cambridge University Press, 153-170.

78. Stager, C. L. and Werker, J. F. 1997, Nature, 388(6640), 381-382.

79. Gillis, S., Schauwers, K. and Govaerts, P. J. 2004, Univ. of Antwerp., Website: http://cnts.uia.ac.be/cnts/ps/20021001.7547.Gillis.doc.10pp.

80. Kuhl, P. K. and Meltzoff, A. N. 1996, J. Acoustical Soc. of America, 100(4), 2425-2438.

81. Ramsdell-Hudock, H. L. 2014, Frontiers in Psych., 5(297). doi:10.3389/fpsyg.2014.00297.

82. Oller, D. K. 2000, The Emergence of Speech Capacity, Lawrence Erlbaum.

83. Tchernichovski, O. and Marcus, G. 2014, Curr. Opinion Neurobiol., 28, 42-7.

84. MacNeilage, P. F. and Davis, B. 2000, Science, 288(5465), 527-531.

85. Brainard, M. S. and Doupe, A. J. 2002, Nature, 417, 351-358.

86. Kuhl, P. K. 2003, Proc. Natl. Acad. Sci., USA, 100, 9645-9646.

87. Ertmer, D. and Mellon, J. 2001, J. Speech, Lang. Hear. Res., 44, 192-206.

88. Stoel-Gammon, C. 1988, J. Speech, Lang. Hear. Res., 53, 302-315.

89. Aronov, D., Andalman, A. S. and Fee, M. S. 2008, Sc., 320(5876), 630-634. doi:10.1126/science.1155140

90. Aronov, D., Veit, L., Goldberg, J. H. and Fee, M. S. 2011, J. Neurosci., 31, 16353-16368.

91. Roberts, T. F., Gobes, S. M. H., Murugan, M., Olveczky, B. P. and Mooney, R. 2012, Nat. Neurosci., 15,1454-1459.

92. London, S. E. and Clayton, D. F. 2008, Nature Neurosc., 11(5), 579-86.

93. Balzer, A. L. and Williams, T. D. 1998, Behav., 135, 297-309.

94. Airey, D. C., Buchanan, K. L., Szekely, T., Catchpole, C. K. and DeVoogd, T. J. 2000, J. Neurobiol., 44(1), 1-6.

95. Leitner, S. and Catchpole, C. 2002, J. Neurobiol, 52, 294-301.

96. Houx, B. B. and ten Cate, C. 1998, Behaviour, 135, 599-614.

97. Madden, J. R., Low, T. J., Fuller, H. V., Dasmahapatra, K. K. and Coe, R. L. 2004, Animal Behav., 68, 759-765.

98. Freeberg, T. M., West, M. J., King, A. P., Duncan, S. D. and Sengelaub, D. R. 2002, J. Comp. Phys. A, 188, 993-1002.

99. Marler, P. and Peters, S. 1982, Acoustic Communication in Birds: Song Learning and Its Consequences, D. E. Kroodsma, E. Miller and H. Ouellet (Eds.), Academic Press, New York, 25-50.

100. Roy, A. and Mooney, M. 2007, J. Neurosc., 27(24), 6374-6387. doi:10.1523/JNEUROSCI.0894-07.2007

101. Vallet, E. and Kreutzer, M. 1995, Animal Behav., 49, 1603-1610.

102. Beecher, M. D. 2016, Animal Behav., 124(2017) 233-246.

103. Elbers, L. 1982, Cognition, 12, 45-63.

104. Piaget, J. and Cook, M. 1952, The Origins of Intelligence in Children, New York: Intern UP, 8(5).

105. Kaplan, G. 2015, Birds Minds, Cognition and Behaviour of Australian Native Birds, CSIRO Publishing, Melbourne.