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Variation in vocal production learning across songbirds

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Songbirds as a whole are considered to be vocal production learners, meaning that they modify the structure of their vocalizations as a result of experience with the vocalizations of others. The more than 4000 species of songbirds, however, vary greatly in crucial features of song development. Variable features include: (i) the normality of the songs of early-deafened birds, reflecting the importance of innate motor programmes in song development; (ii) the normality of the songs of isolation-reared birds, reflecting the combined importance of innate auditory templates and motor programmes; (iii) the degree of selectivity in choice of external models; (iv) the accuracy of copying from external models; and (v) whether or not learning from external models continues into adulthood. We suggest that because of this variability, some songbird species, specifically those that are able to develop songs in the normal range without exposure to external models, can be classified as limited vocal learners. Those species that require exposure to external models to develop songs in the normal range can be considered complex vocal learners.

This article is part of the theme issue 'Vocal learning in animals and humans'.

1. Introduction

When human infants learn new words or juvenile songbirds learn new songs, they acquire the acoustic structure of these vocalizations by listening to adult vocalizations [1]. This behaviour has been termed 'vocal production learning', defined by Janik & Slater [2, p. 1] as 'instances where the signals themselves are modified in form as a result of experience with those of other individuals'. Vocal production learning in this sense has been thought to be confined to just a few taxa outside of humans and songbirds: hummingbirds and parrots among birds, and cetaceans, bats, elephants and pinnipeds among mammals [3–5]. All other taxa, including all non-human primates, have been considered to lack vocal production learning [3,6,7]. This paradigm has been criticized recently, however, with some arguing for the recognition of additional taxa as vocal learners [8–11] and, concomitantly, for the recognition of multiple levels of vocal production learning [4,12–14]. Here, we consider how these new ideas apply to a traditionally recognized group of vocal learners: the 'oscine' songbirds (suborder Passeri). Although songbirds as a whole are considered to meet all criteria for vocal production learning, the 4000 plus species in this clade actually show a wide range of vocal development strategies. Some songbird species tick all the boxes for vocal production learning (hereafter 'vocal learning'), but others fulfill only a subset of the criteria, if that. Below, we first describe some of the new evidence on vocal development in mammals that has led to calls for recognizing levels of vocal learning. We then review what is known about song learning in songbirds, first describing the 'canonical' pattern of song development found in some of the best-studied songbirds and then examining variations on this pattern found across songbirds. We end by describing three recently proposed schemes for recognizing levels of vocal learning and considering how well these schemes fit with variation among songbirds.

2. Are there different levels of vocal learning?

The first criticisms of the binary view of vocal learning (either you have it or you do not) emerged from studies of non-human primates. Non-human primates were originally designated as vocal non-learners [6,7], based primarily on observations of vocal development early in life from a very few species, including evidence that certain primate vocalizations change little between the first days of life and adulthood [15–17], that young primates subjected to social isolation or deafening nevertheless develop normal vocalizations [17], and that infants cross-fostered with another species develop the vocalizations of their genetic rather than their foster parents [18]. By contrast, much of the data suggesting the need for re-evaluation of primate vocal learning came from studies of vocal plasticity in adults [7], where adult call characteristics were found to converge in social groups or mated pairs [19–21]. More recently, evidence has also been found for vocal production learning in primates during early development, for example through the effect of contingent vocal feedback from adults on vocal maturation in marmoset monkeys (*Callithrix jacchus*) [10,22]. Finally, learning of novel auditory signals has been suggested for some great apes [9], in which captive young are more likely to share non-vocal sounds with their mother when raised with her than when raised apart [23]. Studies of the house mouse (*Mus musculus*) have also prompted calls for re-evaluating binary classifications of vocal learning [8], although for mice some experimental results are debated, for example, as to whether deafening does [8,12] or does not [24,25] affect the structure of their ultra-sonic ‘songs’ [26].

Several proposals have been made for recognizing multiple levels of vocal production learning [4,12–14], largely aimed at recognizing intermediate levels of learning that would accommodate the new primate and mouse results. To be successful, however, these proposals must accommodate variation in learning in traditionally recognized vocal learners as well as these putative new cases. Before addressing these proposals, we first describe variation in learning strategies found in the largest group of established vocal learners, the songbirds. Songbird song was traditionally considered a predominantly male trait, functioning in both mate attraction and territorial defence [27,28]. It has been shown recently that female song is widespread, especially among tropical songbirds, and that singing by both sexes is probably the ancestral condition [29]. Song development in female songbirds, however, has received relatively little attention [30], so we focus our review on males.

3. Song development in songbirds: the canonical pattern

Modern research on birdsong learning began with William Thorpe’s application of the sound spectrograph to the study of vocal development in chaffinches (*Fringilla coelebs*) [31,32]. Thorpe’s study of chaffinches was followed by the work of his student, Peter Marler, first on white-crowned sparrows (*Zonotrichia leucophrys*) [33] and then more extensively on song sparrows (*Melospiza melodia*) and swamp sparrows (*Melospiza georgiana*) [34–36]. These four species share a similar pattern of song development, which we will describe as the ‘canonical pattern.’ In all four species, the backdrop for song development is a typical songbird life history, in which breeding is performed by socially monogamous pairs, with young leaving their parents’ territory soon after fledging and then reaching sexual maturity the following spring, when they are approaching one year of age.

The fundamental evidence for song learning in these canonical species stems from two kinds of results. First, individuals that are experimentally isolated during early development and thus prevented from hearing conspecific songs, produce abnormal songs as adults [32,33,37–40] (figure 1). Second, individuals raised in social isolation from adults, but exposed to recordings of conspecific songs, develop songs that resemble natural songs much more closely than do isolate songs [32–34,41] (figure 1). Together, these findings show that exposure to external song models is necessary and sufficient for normal song development.

Although abnormal in many ways, the songs of isolate individuals of our canonical species nevertheless resemble natural song in some respects [31,33,38]. The isolate songs of song sparrows and swamp sparrows, for example, show differences that parallel differences between the natural songs of the two species [38]. For example, isolate songs are divided into more phrases in song sparrows than in swamp sparrows, just as natural songs are divided into more phrases in song sparrows than in swamp sparrows, and so forth. The resemblance of isolate song to natural conspecific song suggests that these canonical species inherit via their genes a template specifying some features of their species-typical song. Additional evidence for an inherited template comes from experiments on selective learning, showing that individuals learn conspecific songs in preference to heterospecific songs when given an equal opportunity to learn from recordings of both [33–35,42]. The fact that socially isolated juvenile birds exposed only to recorded songs prefer to learn conspecific song suggests that the innate template for the song is an auditory representation.

All four canonical species show evidence of a limited period of life—termed the sensitive period—in which they are open to learning from external models [32,33,43–45]. In swamp sparrows, for example, most songs are learned early, from 15 to 55 days post-hatching, but with some learning occurring as late as 300 days [45]. Song sparrows and white-crowned sparrows show similar timing [33,43,44], whereas in chaffinches learning extends later, up to approximately one year [32,46]. In song sparrows, the sensitive period may be extended under natural conditions compared to what is found in the laboratory [47], but still no new songs are added once adulthood is reached [48].

In all four canonical species, the adult song emerges in a series of stages [32]: first, a highly variable ‘subsong’ stage, followed by an intermediate ‘plastic song’ stage, and ending with the final ‘crystallized song’ [49]. Hand-reared swamp sparrows produce subsong sporadically during their first summer and autumn, stop singing altogether during winter, and then start singing again at about 260 days, first with subsong, advancing to the plastic song at about 300 days, and to the crystallized song at about 330 days [50]. In at least two of the four species, a biased set of syllables are dropped as song crystallizes, in a process termed ‘selective attrition’ [51,52].

Konishi [53] found that white-crowned sparrows deafened early in life produce songs that lack almost all features present in natural songs. This result is obtained both if the birds are deafened early in their sensitive period and if they are deafened after having completed their sensitive period with ample exposure to conspecific song. By contrast, deafening had little effect on song once subjects have begun to sing crystallized songs. From these results, Konishi [53] concluded

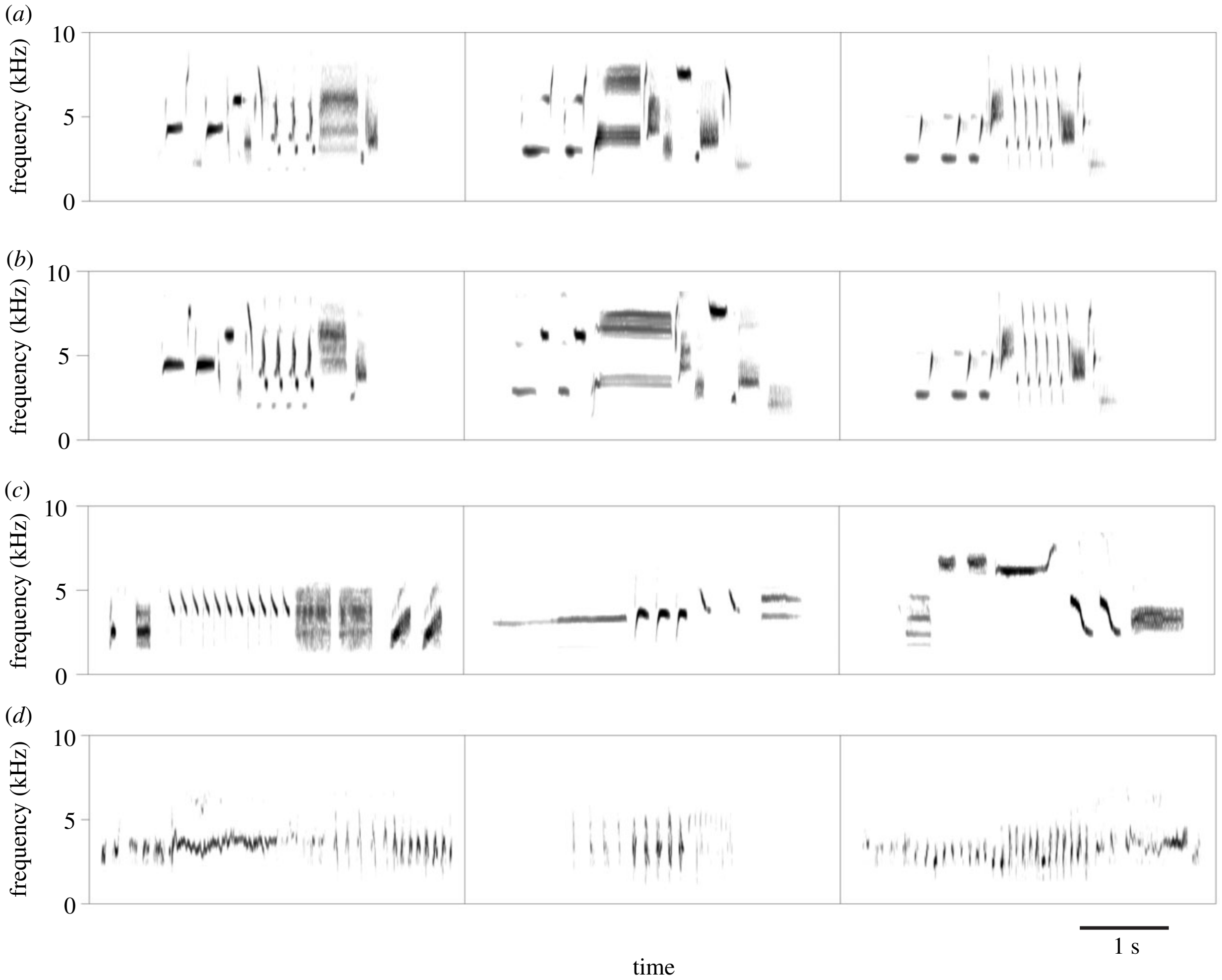

Figure 1. Spectrograms of four categories of song sparrow songs. (*a*) natural songs: three songs recorded in a New York population give some idea of how variable songs are within populations. (*b*) copies: songs recorded from birds isolated in the laboratory and trained with recorded songs including the natural songs in the row above. (*c*) isolate songs: songs produced by hand-reared males prevented from hearing any adult conspecific songs during song development. (*d*) deaf songs: songs produced by males surgically deafened early in song development.

that auditory feedback is required for a bird to match its song output to its auditory template. Nottebohm [54] found a similar pattern in chaffinches. In song and swamp sparrows, songs of early-deafened males are more abnormal than are isolate songs (figure 1) but nevertheless retain some species-typical features; for example, deaf songs are divided into more phrases in song sparrows than in swamp sparrows, paralleling the differences shown by natural and isolate songs in these two species [36].

4. Variation in song development across songbirds

Song development has been studied in only a small fraction of the 4000 plus songbird species; even so, many variations on the canonical pattern have been discovered. Below, we review what is known about variation in song development in songbirds, emphasizing those aspects that might affect how species are classified in terms of levels of vocal learning. Figure 2 summarizes the course of song development and indicates steps where variation occurs.

(a) Variation in the song of early-deafened birds

The songs of birds deafened early in life, before the start of the subsong stage, cannot be affected by either external models or by innate auditory templates, and are therefore thought to reflect motor biases [55,56]. The normality of the songs of early-deafened birds varies widely among songbirds, as shown in the first-ever study of the effects of deafening on song development, performed by Masakazu Konishi [57]. Early-deafened dark-eyed juncos (*Junco hyemalis*) produced songs with the simple temporal structure typical of this species, in which a single syllable is repeated in a steady-rate trill. Early-deafened yellow-eyed juncos (*Junco phaeonotus*), by contrast, did not replicate the more complex temporal pattern typical of their species, in which trills combine with unrepeated syllables in a multi-part song.

Songs of early-deafened birds can also preserve more subtle features of wild-type song. In zebra finches, for example, the middle syllables of a song are normally of higher frequency than the beginning and ending syllables, and this pattern is also found in the songs of early-deafened birds [55]. In canaries, higher level syntactical rules are followed in the songs of early-deafened males as in the songs of birds undergoing normal development [58].

(b) Variation in isolate song

Isolation experiments have been carried out in a number of species of songbirds, with a range of conclusions being reached on the abnormality/normality of the resulting isolate songs. These conclusions should be assessed with some skepticism, however, when based solely on the subjective

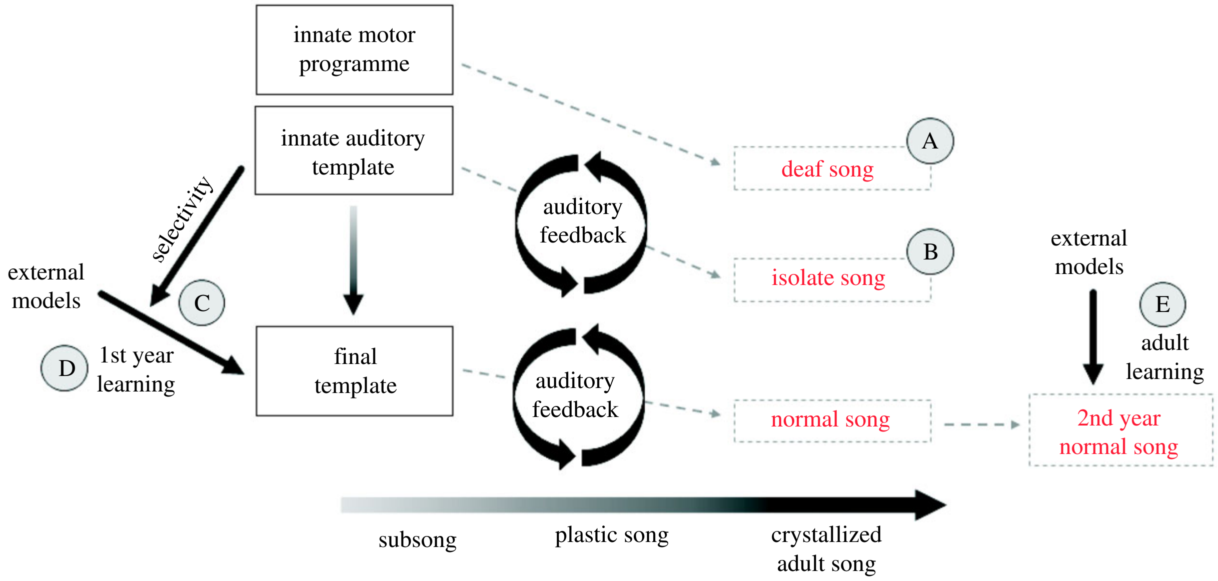

Figure 2. A diagrammatic representation of song development in songbirds. Letters A–E indicate five aspects of development that vary among species: (A) the degree of normality of deaf songs; (B) the degree of normality of isolate songs; (C) selectivity in choice of external models for song learning; (D) accuracy of copying from external models; (E) whether learning from external models continues during adulthood.

judgements of the researchers. Song sparrows provide a cautionary tale in this regard.

Mulligan [59] studied the songs of three song sparrows that were hatched and raised by canaries (*Serinus canarius*) and then housed together in group isolation. Based on subjective inspection of sound spectrograms, Mulligan concluded that the songs of these birds were essentially normal. Although he hedged that statement in various ways, the conclusion others took from this study was that song sparrows do not require exposure to conspecific models to produce normal song (e.g. [33,54]. Subsequent studies examined songs produced by song sparrows reared in isolation from conspecific juveniles as well as from adults; the resulting isolate songs were found to be quite abnormal, based both on quantitative analysis of acoustic measurements [37,38] and on measurement of receiver response to the songs [37,60]. Mulligan's conclusion was thus reversed, and song sparrows are now cited as a species that depends on conspecific models to produce normal song [61].

The song sparrow example suggests that the normality of isolate songs needs to be assessed in an objective fashion, ideally using a procedure that can be standardized across species. Love *et al.* [61] attempted such an analysis, using data from isolation studies in 15 songbird species. The data were mainly generated by converting published spectrograms back into sound files and analysing those. Love *et al.* split song measurements into three modules, designed to separate song features affected by different parts of the song production system; these modules were syllable morphology, song rhythm and song syntax (i.e. the sequencing of song elements). All the species examined by Love *et al.* showed some abnormality in at least one module, but there was considerable variation across species in the degree of abnormality. At one extreme, isolate songs of song sparrows were the most abnormal of the 15 species in both syllable morphology and rhythm and were also moderately abnormal in syntax. At the other extreme, the isolate songs of northern cardinals (*Cardinalis cardinalis*) were rated as normal in syllable morphology and rhythm, and as only slightly abnormal in syntax. Dittus & Lemon [62], whose study produced the isolate cardinal songs, came to a parallel conclusion, stating that isolate songs of northern cardinals 'are typical of their species in terms of overall frequency, temporal pattern, quality and organization' [62, p. 530], without mentioning any way in which they are abnormal.

Two additional songbird species have been cited as producing isolate songs that are basically normal [63]. One of these is the gray catbird (*Dumetella carolinensis*), which is said to produce 'apparently normal' songs with no exposure to external models [64]; however, the songs of only a single isolation-reared individual were analysed in this species. The second species is the sedge warbler (*Acrocephalus schoenobaenus*). Leitner *et al.* [65] compared four sibling pairs of sedge warblers with one member of each pair isolated from the conspecific song during development and the other trained with recordings of the conspecific song. The songs of the isolate birds did not differ significantly from the songs of their tutored siblings in a number of syllable types per song, the number of syllables per song, or song length, and overall were said to be 'surprisingly normal in terms of their detailed structure' [65, p. 2522].

(c) Variation in selectivity

Some authorities have argued that the strongest evidence for vocal learning is the ability to copy sounds that are not in a species' normal repertoire [3,13]. Swamp sparrows fail this criterion, in that when tutored with equal number of song sparrow and swamp sparrow songs, they exclusively copy their own species' songs [34]. Even stronger selectivity has been demonstrated in white-crowned sparrows, in that individuals of at least one population prefer learning songs of their own subspecies over songs from another white-crowned sparrow subspecies [66]. White-crowned sparrows can, however, be induced to copy portions of heterospecific songs by tying them to an introductory whistle from a white-crowned sparrow song and can also learn full heterospecific songs that begin with whistles of their own; the whistle thus serves as a marker of what sounds are acceptable for copying [42]. At the other end of the selectivity spectrum, an estimated 9% of all songbird species regularly incorporate vocalizations of other species and/or environmental sounds in their vocal repertoires [67]. Examples of species that incorporate sounds from other species in their songs include northern mockingbirds (*Mimus polyglottos*), European starlings (*Sturnus vulgaris*) and superb lyrebirds (*Menura novaehollandiae*) [68–70].

(d) Variation in copy accuracy

Copy accuracy is another aspect of vocal development that varies among songbirds and that might affect how species are classified in terms of levels of learning. High copy accuracy can be seen in laboratory-reared song sparrows in the detailed resemblance of some of their songs to specific models they were trained with (figure 1). High copy accuracy is the norm among free-living males in the western population of song sparrows studied by Beecher and colleagues, with young males typically copying in detail entire songs of older males [71,72]. Other species that are capable of accurate and detailed copying of complex songs include canaries [73], zebra finches (*Taeniopygia guttata*) [74] and nightingales (*Luscinia megarhynchos*) [75]. At the other end of the spectrum, grasshopper sparrows (*Ammodramus savannarum*) [76], yellow-eyed juncos [77] and some populations of sedge wrens (*Cistothorus platensis*) [78] need to hear conspecific models in order to develop songs in the normal range, but do not copy the details of any one model.

Cases in which song development is influenced by external models without accurate copying of a particular model can be attributed to a variety of processes, including (i) inaccurate memorization of an external model, (ii) improvization, in which a bird's own song gradually diverges from an accurately memorized model, and (iii) invention, in which a bird creates a new song that obeys conspecific conventions without copying the details of any specific model [49]. Which of these processes predominates can vary between species [49,78].

(e) Variation in adult plasticity

Previous reviews of variation in song learning across songbirds have given much attention to variation in the timing of the sensitive period during which individuals learn from external models [63,79]. One question has been the timing of the sensitive period relative to natal dispersal, which has implications for the functional significance of song dialects [80,81]. A second question has been whether song learning continues into adulthood, so that adult song exhibits some degree of plasticity. It is this second question that is relevant to comparisons with other putative vocal learners, such as primates.

If a species' song repertoire is fixed at the age when adulthood is reached, in the sense that no new song types or syllable types are subsequently added, this constitutes strong evidence against song learning by adults. Robinson *et al.* [82] found that 38 of 67 songbird species for which they could find data had adult repertoires that were fixed in this sense. Species with fixed adult repertoire include our four canonical species plus such well-studied species as the field sparrow (*Spizella pusilla*) and the medium ground finch (*Geospiza fortis*) [83,84]. Most songbird species reach adulthood at 1 year of age, and that is the age by which the song repertoire stabilizes. A few species have an earlier age of first reproduction (notably zebra finches), and in these, the song repertoire stabilizes earlier; conversely, in species with a later age of first reproduction the song repertoire stabilizes later than 1 year [85–87].

In the remaining 29 species examined by Robinson *et al.* [82], song repertoires change during adulthood. In red-winged blackbirds, for example, a male retains his previous song types from year to year while continuing to add new ones up to the age of 3 or 4 [88,89]. Canaries change their repertoires more radically from one year to the next by dropping a large proportion of their syllables between breeding seasons and adding enough new ones that the overall repertoire size increases [90]. The tropical clay-coloured thrush (*Turdus grayi*) similarly changes a large proportion of its syllable repertoire between years but also changes a smaller proportion within breeding seasons [91]. Phylogenetic analysis indicates that within the songbirds there have been numerous transitions both from adult song stability to adult song plasticity and in the opposite direction, from plasticity to stability [82]. Adult song plasticity is associated with larger song repertoires, suggesting that vocal learning in adulthood facilitates the acquisition of larger repertoires [82].

Song types that researchers label as new in a 2- or 3-year-old male may actually have been memorized before the age of 1 year and then not produced during the first breeding season [91]. Work with European starlings has shown that they are indeed capable of storing models in memory for up to 18 months without production [92]. Thus, to demonstrate adult song learning conclusively, one needs to show experimentally that song models initially presented to birds well into adulthood are subsequently incorporated in their repertoires. These requirements have been met in only a few studies of captive birds [88,92,93] and to a limited extent in field experiments [94]. Adult song learning may occur, of course, in many songbird species in which it has not yet been conclusively demonstrated. Nevertheless, it is clear that, whereas in non-human primates vocal learning seems more widespread in adults than in juveniles, the opposite is true in songbirds.

5. Songbirds and levels of vocal production learning

We next consider how variation in song learning across songbirds fits with proposed schemes for delineating levels of vocal production learning. The simplest such scheme, proposed by Tyack [13], recognizes two levels: limited vocal learning, in which vocal learning is limited to fine-tuning acoustic features of vocalizations that are controlled by innate motor programmes, and complex vocal learning, defined by the need to hear an external model before being able to develop a vocalization that matches the model. Tyack comments that 'the critical point for distinguishing complex from limited vocal learning is whether subjects require auditory input to develop their normal species-specific vocalizations, or whether a central motor programme allows these to develop in the absence of auditory input' [13, p. 7]. In songbirds, the songs of early-deafened birds are usually assumed to be the product of innate motor programmes. These deaf songs are never fully normal, as far as is known, so innate motor programmes apparently are never sufficient for normal song development. Nevertheless, deaf songs often do have some species-typical features, indicating that innate motor programmes may play some role in song development. Furthermore, there appear to be cases in which isolate songs are fully normal, suggesting that some songbirds can develop normal songs without any input from external models. Such cases seemingly would not qualify under Tyack's definitions as either limited vocal learning (since an innate motor programme is not sufficient to bring the song into the normal range) or complex vocal learning (since an external model is not necessary to develop a normal song). Thus, for songbirds, we suggest changing the definition of limited vocal learning to the fine tuning of acoustic features, in response to external models, of vocalizations that develop within the normal conspecific range without exposure to external models. This change allows development within the normal range without external models to be accomplished by innate auditory templates as well as by innate motor programmes or by some combination of both.

Arriaga & Jarvis [12] proposed what they dubbed the 'continuum hypothesis', which makes an initial division similar though not identical to Tyack's, separating cases in which vocalizations are based on an innate motor template (category 1) from those in which vocalizations are 'generated *de novo*' (category 2). Within category 1, four levels of plasticity are recognized, from (1a) none, to (1b) plasticity in amplitude and temporal structure, (1c) modification of spectral features as well as amplitude and temporal structure without an externally acquired target, and (1d) modification of spectral, amplitude and temporal features influenced by an externally acquired target. Within category 2 (generated *de novo*), acoustic features including spectral ones are modified either without reference to an externally acquired model (level 2a) or with reference to such a model (level 2b). A strict application of these criteria would relegate most songbirds to category 1, given that in most songbird species studied to date song development involves both innate motor programmes and innate auditory templates. More specifically, most songbirds would be consigned to category 1d of the continuum hypothesis, in which the acoustic features of template-based vocalizations are modified with reference to an external model. Arriaga and Jarvis state explicitly, however, that they consider 'song learning birds' to belong in category 2b, the category intended for species with vocalizations that are generated *de novo* and that modify those vocalizations with reference to external models. We suggest it is not justifiable to claim that songbird songs are generated *de novo* if the form of those songs is constrained to a greater or lesser degree by innate motor programmes and auditory templates. Overall, the continuum hypothesis does not perform well in categorizing song learning in songbirds.

Wirthlin *et al*. [14] criticize the continuum hypothesis for implying that vocal production learning evolves along a single trajectory. They propose instead to divide vocal learning into three modules that evolve independently, so that improvements in the modules can evolve in different sequences in different lineages. Their first module concerns vocal coordination between individuals, as seen in behaviours such as antiphonal calling, duetting and chorusing. The development of vocal coordination is beginning to attract more attention in songbird research (e.g. [95]), but strictly speaking is not an aspect of vocal production learning, but rather of usage learning [2]. Wirthlin *et al*.'s second module, 'vocal production variability', describes how a species changes the variability of its vocal output during successive stages of development, for example by going through a subsong or babbling stage, but this in itself does not necessarily delineate different levels of vocal learning ability. Their proposed third module, vocal versatility, comprises variation along two axes: vocal diversity, in the sense of vocal repertoire size and vocal plasticity, the degree to which vocalizations can be modified. Here the authors are mainly concerned with different levels of control over sound sources (syrinx or larynx) and sound filters (the post-source vocal tract). Presumably all songbirds are able to control both source and filter during vocal development, but this distinction might be valuable for other taxa.

6. Conclusion

Any scheme for recognizing levels of vocal production learning needs to accommodate the range of song development strategies found in songbirds. None of the three schemes described above do well in this regard, perhaps because they were developed to deal with new, minimal cases of vocal learning rather than with older, robust ones. The existing scheme that fits best with songbirds, perhaps because it is the simplest, is that of Tyack [13], but this scheme needs to be adjusted for songbirds by recognizing that it is possible to develop normal vocalizations without external input using an innate auditory template rather than an innate motor programme. We thus suggest a revised version of Tyack's scheme as follows:

(i) vocal non-learning—normal conspecific vocalizations develop without input from external models and without subsequent fine tuning of those vocalizations through the influence of external models;
(ii) limited vocal learning—normal conspecific vocalizations can develop without input from external models, but subsequent fine tuning of those vocalizations through the influence of external models can also occur; and
(iii) complex vocal learning—normal conspecific vocalizations develop only through the influence of appropriate external models.

An additional category that could be added to this scheme is one in which individuals adjust their vocalizations by comparing their vocal output to an internal auditory template but not to any external model. This change would subdivide the vocal non-learning category into species that use an innate motor programme and species that (also) use an innate auditory template. At present, however, we know of no species that would fit the criteria for this new category, namely that the species' isolate songs are in the normal range, its deaf songs are abnormal, and it fails ever to show any effects of experience with external models. If such cases are discovered, they might be designated as self-referential vocal learners. Such cases would be important, as they would increase the plausibility of self-reference having evolved the before reference to external models.

We understand that our proposed modification of Tyack's scheme may not satisfy researchers attempting to connect evidence for vocal plasticity to song learning in songbirds, especially when the effects of that plasticity are relatively small as compared to the nearly eidetic copying of external models displayed by some birds. Nonetheless, we hope that a more complete understanding of how variable patterns of song learning can be across songbird species, beyond the 'canonical' model found in most textbooks, will provide a useful stepping-stone towards a more synthetic understanding of vocal plasticity in general.

Data accessibility. This article has no additional data.

Authors' contributions. W.A.S. and S.N. outlined the paper, after which all authors contributed to reference research and conceptual organization of the material. W.A.S. wrote the initial draft and all other authors contributed to editing and production of the final draft.

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