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Birdsong learning, avian cognition and the evolution of language

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The most language-like aspect of the song of songbirds is its development: as with human speech, birdsong develops through vocal production learning, in which individuals modify the structure of their vocalizations in response to experience with the vocalizations of others. As is true of speech development, birdsong learning qualifies as a cognitive ability, as it involves the acquisition, storage and processing of information obtained from the environment. Accordingly, if cognitive abilities are in general positively associated in songbirds, as has been argued for humans and other mammals, then song learning ability should be positively associated with other cognitive abilities, and learned attributes of song should serve as an indicator of domain-general cognition. A review of studies in which songbirds have been subjected to batteries of cognitive tasks finds, however, that different cognitive measures are not consistently positively associated. Moreover, learned attributes of birdsong do not show consistent positive associations with other cognitive measures. These results argue that, rather than being a component of domain-general cognition, song learning is an autonomous cognitive module. Birdsong learning shows other characteristics of modularization in that it is domain specific, is based on a localized and highly structured neural system and exhibits a level of innate specification. Whether language learning in humans is similarly modularized has been much debated. Despite a possible difference in modularization, much can be learned about the evolution of human language learning from studying birdsong learning. Aspects of birdsong learning that are especially relevant include vocal interaction learning, pragmatics and the initial selective benefits and neural underpinnings of vocal production learning.

Although birdsong is in some respects a complex behaviour, in terms of cognition it is for the most part relatively simple. Across songbirds, song has a simple message, or rather two simple messages directed at different audiences: an aggressive, 'keep-out' message directed at same-sex conspecifics and an advertisement, mate attraction message directed at opposite-sex conspecifics (Catchpole & Slater, 2008; Searcy & Andersson, 1986; Tinbergen, 1939). The intensity of these messages can be modulated in some species, for example by changing song type (Byers, 1996) or amplitude (Akçay, Anderson, Nowicki, Beecher, & Searcy, 2015), but the message is not changed qualitatively. Because the information conveyed by song concerns the singer (e.g. its species, mating status, condition, aggressiveness, etc.), birdsong lacks one of the chief attributes that Hockett (1960) required of abstract symbols: it does not refer to features or situations of the world external to the signaller. Birdsong also lacks two additional attributes that Hockett considered necessary for symbols: it is not used to refer to things displaced in time or space from the signaller, and its meaning is not always arbitrary with respect to its physical features (Ballentine, 2009; Ryan & Brenowitz, 1985).

Birdsong is simple syntactically as well as semantically. Birdsong exhibits syntax in that smaller elements can be assembled into larger wholes — notes into syllables, syllables into songs, and songs into bouts — with rules of varying complexity on what sequences are allowable (Berwick, Okanoya, Beckers, & Bolhuis, 2011). Birdsong does not, however, exhibit compositional syntax (Hurford, 2011), a feature of human languages in which meaningful sounds (i.e. words) are combined in different orders to generate new meanings. Evidence for compositional syntax has recently been found for combinations of alarm calls and recruitment calls in Japanese great tits, *Parus minor* (Suzuki, Wheatcroft, & Griesser, 2016), and southern babblers, *Turdoides bicolor* (Engesser, Ridley, & Townsend, 2016), but we are aware of no such evidence for

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song in. any songbird. Thus, in terms of syntax as well as semantics, birdsong is relatively simple and not at all language-like.

Only with respect to development is birdsong both cognitively complex and language-like. Song in songbirds is learned. More specifically, birdsong develops through vocal production learning, defined by Janik and Slater (2000, p. 2) as 'instances where the signals themselves are modified in form as a result of experience with those of other individuals'. This definition distinguishes vocal production learning from other categories of vocal learning, such as vocal usage and comprehension learning (Janik & Slater, 2000). Vocal production learning allows transmission through cultural tradition, which is another of the design features ascribed by Hockett (1960) to human language. It is because the songs and some of the calls of birds are learned that Darwin (1871, p. 55) concluded that 'the sounds uttered by birds offer in several respects the nearest analogy to language … ' found in nonhuman animals. Darwin's conclusion might have been different if he had known about subsequent discoveries on primate vocalizations (Seyfarth, Cheney, & Marler, 1980) and bee dances (von Frisch, 1967), but nevertheless serves to emphasize that it is in vocal learning that birdsong has its greatest relevance to human language.

A central question when considering the relevance of birdsong learning to the evolution of cognition and language is whether to interpret song learning as a cognitive module independent from other cognitive abilities or as an integral part of general intelligence. This question will be the primary focus of the present paper. We start by reviewing the phylogenetic distribution of vocal production learning. We then make the argument that song learning in songbirds qualifies as a cognitive ability. Next, we explain the distinction between domain-general and modularized views of cognition and how this distinction applies to birds. We then review existing evidence on the association of song learning ability with other cognitive abilities. The results support the absence of such an association, which in turn supports the interpretation of song learning as an independent cognitive module. We end by considering what song learning in songbirds can teach us about the evolution of human language.

PHYLOGENETIC DISTRIBUTION OF VOCAL LEARNING

The occurrence of well-developed vocal production learning is phylogenetically quite restricted. No instances are known outside birds and mammals. Among birds, vocal production learning is well established in just three groups (Fig. 1): hummingbirds (Araya-Salas & Wright, 2013; Gaunt, Baptista, Sanchez, & Hernandez, 1994), parrots (Berg, Delgado, Cortopassi, Beissinger, & Bradbury, 2012; Pepperberg, 1981) and songbirds (Beecher & Brenowitz, 2005). The hummingbirds (family Trochilidae) are fairly distantly related to the other two groups (Fig. 1) (Jarvis et al., 2014; Prum et al., 2015), suggesting a minimum of two origins of vocal production learning within the birds. Parrots (order Psittaciformes) are now thought to be the sister clade of the passerines (Fig. 1), the order that includes songbirds (suborder Passeri). Separating the parrots from the songbirds, however, is another passerine group, the suboscines (suborder Tyranni), within which there is firm experimental evidence against vocal production learning in two families, tyrant flycatchers (Kroodsma, 1989; Kroodsma & Konishi, 1991) and antbirds (Touchton, Seddon, & Tobias, 2014), and indirect evidence in favour of vocal production learning in another, the cotingas (Kroodsma et al., 2013; Saranathan, Hamilton, Powell, Kroodsma, & Prum, 2007). Given this phylogenetic distribution, it is not yet clear whether vocal production learning evolved multiple times within the parrot/passerine clade or evolved once at the base of the clade with one or more losses later occurring within the suboscines.

Vocal production learning has been shown to occur in five groups of placental mammals (Fig. 2): cetaceans (Janik, 2014; King, Sayigh, Wells, Fellner, & Janik, 2013), bats (Boughman, 1998; Knörnschild, 2014), pinnipeds (Reichmuth & Casey, 2014), elephants (Poole, Tyack, Stoeger-Horwath, & Watwood, 2005; Stoeger et al., 2012) and humans. The phylogenetic distribution of vocal production learning in mammals suggests multiple origins of the trait (Fig. 2). Arguments have been made recently for the occurrence of limited instances of vocal production learning in species of nonhuman primates (Lameira, 2017; Lameira, Hardus, Mielke, Wich, & Shumaker, 2016; Lemasson, Ouattara, Petit, & Zuberbühler, 2011; Takahashi et al., 2015) and hence for relaxing the binary distinction between vocal learners and nonlearners (Petkov & Jarvis, 2012). Nevertheless, the traditional conclusion that vocal production learning is poorly developed in primates other than humans (Egnor & Hauser, 2004; Janik & Slater, 1997; Snowdon, 1990) seems likely to stand. Because of the limited occurrence of vocal production learning in primates and its importance to language in humans, Fitch (2017) designated this ability as one of three 'derived components of language', key innovations that are essential for language and that evolved after humans split from their closest living relatives.
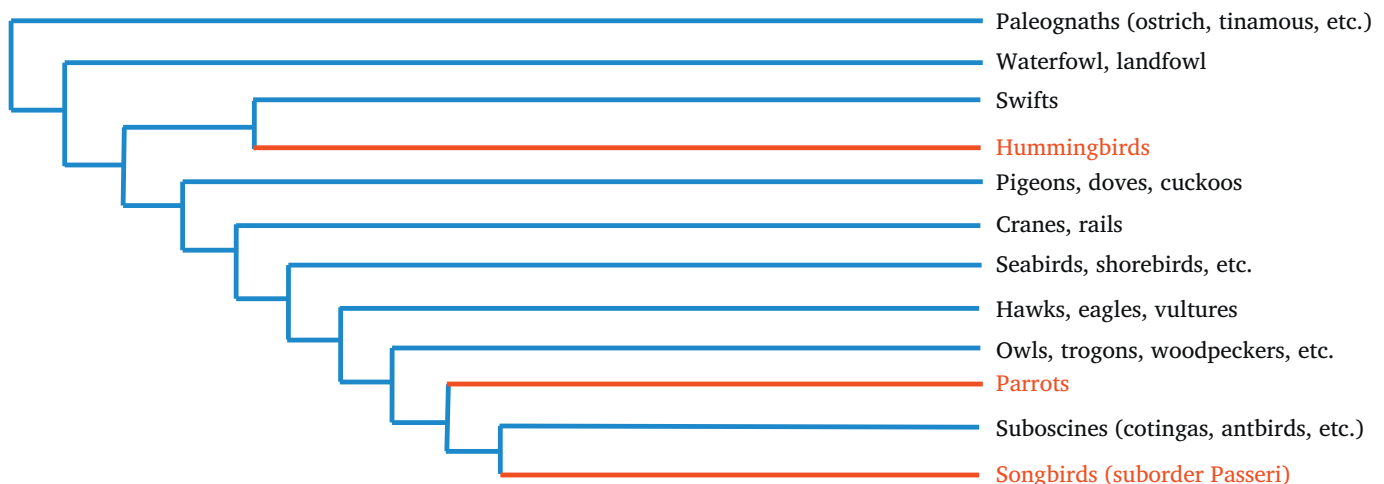

Figure 1. Phylogenetic distribution of vocal production learning in birds. Red indicates lineages in which vocal production learning is known to occur. Phylogenetic hypothesis simplified from Prum et al. (2015) with many taxa omitted.
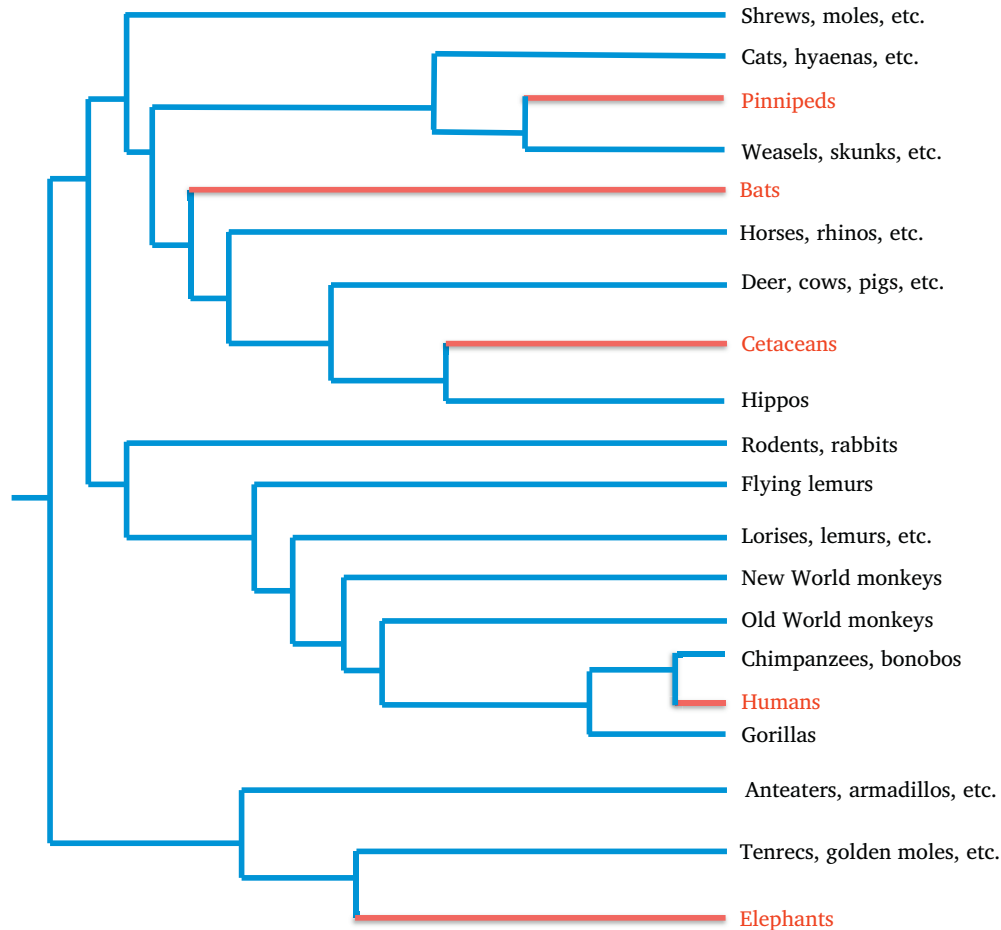
Figure 2. Phylogenetic distribution of vocal production learning in mammals. Red indicates lineages in which vocal production learning is known to occur. Phylogenetic hypothesis simplified from Meredith et al. (2011) with many taxa omitted.

Vocal production learning evidently is not homologous in humans and songbirds; that is, the ability has not been inherited by both groups from a common ancestor (Fitch, 2017). This conclusion does not imply that vocal learning in songbirds can tell us nothing about the evolution of vocal learning in humans. Detailed similarities with human language learning are better established for song learning in songbirds (Brainard & Doupe, 2002; Doupe & Kuhl, 1999; Marler, 1970a) than for vocal production learning in any other taxon. The evolution of vocal production learning in humans and songbirds represents convergence rather than homology, but convergence can teach us much about the selective forces and environmental conditions leading to the evolution of a trait (Losos, 2011).

SONG LEARNING AS A COGNITIVE TASK

Definitions of cognition vary, but one that is often used in studies of animal cognition is from Shettleworth (2010, p. 4): 'Cognition refers to the mechanisms by which animals acquire, process, store, and act on information from the environment. These include perception, learning, memory, and decision-making'. Presumably a task that uses any one of these abilities would be considered cognitive, but in fact birdsong learning uses them all. We give evidence for this claim drawn especially from two species that we have studied, song sparrows, *Melospiza melodia*, and swamp sparrows, *Melospiza georgiana*.

Perception is a prerequisite for song learning in that young songbirds must hear singing adults to acquire information on the correct form of their species-typical song. Evidence for this conclusion is that young birds isolated at an early age to prevent them from hearing conspecific song develop songs that are highly abnormal, as shown by Kroodsma (1977) for song sparrows and Marler and Sherman (1985) for swamp sparrows, following earlier demonstrations by Thorpe (1958) and Marler (1970b) for chaffinches, *Fringilla coelebs*, and white-crowned sparrows, *Zonotrichia leucophrys*, respectively. Laboratory-reared birds presented with song models, from either recorded song or live tutors, develop songs that are much more normal, often incorporating fine details from model songs (Marler & Peters, 1977, 1981, 1987; Nowicki, Searcy, & Peters, 2002b).

Perceptual memory also plays a role in song learning in that the details of model songs are stored in memory between the sensory period in which the young bird hears the models and the sensorimotor phase in which it rehearses them. These two phases overlap in some songbirds (Brainard & Doupe, 2002), but are separated by a definite gap in the sparrows we study. Marler and Peters (1982a) measured the duration of this gap in swamp sparrows by tutoring captive birds for 2 months posthatching and then recording them at weekly intervals from 90 to 400 days. The mean gap between the last exposure to the training songs and the first production of imitations was 237 days (range 203—275). Swamp sparrows thus retain the details of model songs in memory for approximately 8 months before using those memories to shape their own songs. Song and swamp sparrows show evidence of having memorized only a modest number of model songs, on average about 10—12 in

the plastic song repertoires of song sparrows (Nordby, Campbell, & Beecher, 2007) and about 12 in swamp sparrows (Prather, Peters, Nowicki, & Mooney, 2010); other species, however, learn far more. Nightingales, *Luscinia megarhynchos*, for example, retain scores of songs in memory for 4 months or more before starting to practise them (Hultsch & Kopp, 1989; Todt, Hultsch, & Heike, 1979).

Information processing occurs during the sensorimotor phase of song learning as the young bird adjusts its own vocal production to match the song models it has in memory. Konishi (1965) showed the importance of this step in white-crowned sparrows by deafening young birds; deafened males developed songs that were even more abnormal than isolate songs even when deafening occurred after exposure to the model songs, as long as it occurred before the male started to sing. Song and swamp sparrows deafened early in life also develop songs that are more abnormal than isolate songs (Marler & Sherman, 1983). Detailed examination in swamp sparrows (Marler & Peters, 1982b) and zebra finches, *Taeniopygia guttata* (Tchernikovski, Mitra, Lints, & Nottebohm, 2001) of the subsong and plastic song stages preceding song crystallization shows song features converging on those of song models, although not always directly. Song sparrows sometimes modify songs between the penultimate plastic song stage and the final, crystallized stage to be less similar to tutor songs, perhaps to promote individual distinctiveness (Beecher, 2017; Nordby et al., 2007).

Decision making plays a role in song learning in choice of song models. At one level, song and swamp sparrows show innate preferences for learning their own species' songs over the songs of the other species. These preferences have been demonstrated in laboratory studies in which isolate males are exposed early in life to equal numbers of recorded song elements of the two species; under these conditions song sparrows show a strong but partial preference for learning song sparrow syllables and phrases (Marler & Peters, 1988), whereas swamp sparrows show a complete preference for their own species' elements (Marler & Peters, 1977). At another level, song sparrows choose which songs to learn and retain among the many conspecific models available to them. Retention is an issue because both song sparrows and swamp sparrows sing more song types in the plastic song stage than they retain in their crystalized repertoires (Marler & Peters, 1982b; Nordby et al., 2007). In nature, a young male song sparrow preferentially learns songs from adult males holding territories in the area where he settles after natal dispersal, showing further preferences for learning or retaining songs that are shared by multiple potential tutors and that are from adults that survive into the next breeding season (Akçay, Campbell, Reed, & Beecher, 2014; Beecher, 2017; Beecher, Campbell, & Stoddard, 1994; Nordby, Campbell, & Beecher, 1999).

Song learning thus includes all the mechanisms that Shettleworth (2010) included in her definition of cognition: learning, obviously, but also perception, memory, information processing and decision making. We conclude that song learning qualifies as a cognitive task, which has implications for how we expect song learning to relate to cognition in general.

GENERAL INTELLIGENCE VERSUS MODULARIZATION

More than a century ago, Spearman (1904) concluded, for humans, that correlations between performance on different cognitive tests are generally all positive, a phenomenon that became known as the 'positive manifold'. Spearman (1904) additionally found that scores on all cognitive tests load positively on the first or dominant factor in factor analyses. Subsequent analysis of larger and larger sets of human cognitive data have reinforced these two empirical generalizations (Carroll, 1993; Jensen, 1998). Spearman (1904) interpreted his results as indicating that a general intelligence factor, or *g*, influences success on all cognitive tests in humans. This interpretation has remained popular (Burkart, Schubiger, & van Schaik, 2017), although alternative explanations for the positive manifold have been advocated that do not assume the existence of general intelligence (Thomson, 1916; van der Maas et al., 2006).

Among nonhuman animals, evidence for a positive manifold is strongest in mice (*Mus musculus*) (Burkart et al., 2017). Matzel et al. (2003), for example, assessed 56 outbred mice on five cognitive tasks, including two types of mazes and passive avoidance, odour choice and fear-conditioning tests. Success was then compared for pairs of tests using simple Pearson correlations. Ten of ten pairwise correlations were positive, although only two were significantly greater than 0. Additional mouse studies also have found uniformly positive correlations between performance scores on different cognitive tasks (Kolata, Light, & Matzel, 2008; Locurto & Scanlon, 1998); other studies have found a mix of positive and negative correlations, but with positive correlations still predominating (Galsworthy et al., 2005; Locurto, Fortin, & Sullivan, 2003). Support for general intelligence has also been found in nonhuman primates such as cottontop tamarins, *Saguinus oedipus* (Banerjee et al., 2009) and chimpanzees, *Pan troglodytes* (Hopkins, Russell, & Schaeffer, 2014). Some authors have suggested that *g* exists in all animals (Plomin, 2001).

Evidence for a positive manifold, however, is weak in birds. Anderson et al. (2017), for example, assessed 41 song sparrows of mixed sexes on tests of a novel foraging skill, colour association, colour reversal, spatial learning and detour reaching. When success on pairs of tests was compared using Spearman rank correlations, only 5 of the 10 correlations were positive, and only one was significantly greater than 0 (between colour association and colour reversal). DuBois, Nowicki, Peters, Rivera-Cáceres, and Searcy (2018) assessed male swamp sparrows on the same five cognitive tasks, with a sample size of 20–49 depending on the correlation, and found only 3 of 10 correlations were positive, with again only the correlation between colour association and colour reversal significant. Keagy, Savard, and Borgia (2011) assessed 20 male satin bowerbirds, *Ptilonorhynchus violaceus*, on five cognitive measures not related to song, and found that only 4 of 10 pairwise correlations between measures were positive, while none of the correlations differed significantly from 0. Other studies finding a mix of positive and negative correlations between cognitive measures include a study of 20 New Zealand robins, *Petroica longipes*, employing five cognitive measures (Shaw, Boogert, Clayton, & Burns, 2015), an investigation of 36 European starlings, *Sturnus vulgaris*, with six measures (Nettle et al., 2015), an investigation of 22 European starlings with four measures (Farrell, Morgan, & MacDougall-Shackleton, 2016) and a study of 31 ring-necked pheasants, *Phasianus colchicus*, with nine measures (van Horik, Langley, Whiteside, Laker, & Madden, 2018). Only a study of Australian magpies, *Cracticus tibicen*, with 47 subjects and four cognitive tests found strong evidence for a positive manifold (Ashton, Ridley, Edwards, & Thornton, 2018).

The absence of a positive manifold in most bird studies is evidence against general intelligence in birds, but with two caveats: sample sizes in these bird studies tend to be smaller than in mouse studies, and most of the relevant bird studies have not tested the repeatability of cognitive assays. The repeatability of cognitive tests in nonhuman animals is in general quite low; a recent meta-analysis found the mean temporal repeatability (for the same test given at different times) averaged over human and nonhuman studies was only 0.183, with the majority of *R* values for nonhuman animals not differing significantly from 0 (Cauchoix et al., 2018). In addition, the choice of cognitive tests in these studies is vulnerable to criticism, both on whether each component test actually

measures cognition and on whether the battery as a whole assesses a sufficient range of cognitive domains (Rowe & Healy, 2014; Shaw & Schmelz, 2017).

An alternative to the hypothesis of general intelligence is the proposal that cognition is organized in modules (Fodor, 1983), where cognitive modules are specialized mechanisms that have evolved to solve specific cognitive problems of adaptive importance (Cosmides & Tooby, 2002; Frankenhuis & Ploeger, 2007; Tooby & Cosmides, 1992). Examples of putative cognitive modules include a kin recognition mechanism in humans to solve the problem of avoiding incest (Lieberman, Tooby, & Cosmides, 2007) and enhanced spatial memory in food-storing birds to aid in relocating caches (Shettleworth, 2003). It has been suggested that a small set of specialized cognitive modules was the ancestral condition in vertebrates, with additional modules having been added incrementally in vertebrate evolution (Burkart et al., 2017). Modules may evolve more easily in response to natural selection than does general intelligence (Burkart et al., 2017; Cosmides, Barrett, & Tooby, 2010), pushing the organization of cognitive architecture in the modular direction.

Cognitive modules may be primary, in the sense that a particular cognitive ability evolved originally as a separate module to address a specific cognitive problem (Burkart et al., 2017). Alternatively, a cognitive ability might emerge from domain-general cognition and then become more modularized during individual ontogeny, as solving the pertinent cognitive problem becomes progressively more automatic (Burkart et al., 2017). The possibility of secondary cognitive modules makes identification of primary cognitive modules more difficult. Song learning, however, has many of the attributes of the classic 'Fodorian module' as laid out by Fodor (1983). These attributes include:

(1) The module is domain specific, in that it addresses one specific cognitive problem. Song learning arguably meets this criterion: the module addresses only the problem of song learning and production.

(2) The module is 'hardwired' in the sense of being associated with a dedicated neural system that is 'localized' and 'highly structured' (Fodor, 1983). Song learning and production in songbirds is famously associated with a highly structured and localized neural architecture consisting of brain nuclei linked by projections into two interacting pathways, a descending motor pathway necessary for both learning and production and an anterior forebrain pathway necessary only for learning (Mooney, 2009; Nottebohm, 2005; Nottebohm, Stokes, & Leonard, 1976).

(3) The module is 'innately specified' as opposed to being 'formed by some sort of learning process' (Fodor, 1983). There is no indication that songbirds learn how to learn songs, so this criterion too seems satisfied.

(4) The module is 'computationally autonomous', by which Fodor (1983) means that it does not share resources such as memory and attention with other cognitive systems. The song system does store song memories, but these also seem to be stored elsewhere (Roberts & Mooney, 2013), making the case for computational autonomy equivocal.

Altogether, song learning does exceptionally well in meeting the criteria for a cognitive module. In particular, the evidence that song learning maps to specific neural units is quite strong compared to evidence on this point for putative cognitive modules in general (Burkart et al., 2017).

Even if song learning is a primary cognitive module, song learning ability might still be associated with other cognitive abilities if both are affected by the same developmental and genetic factors (Peters, Searcy, & Nowicki, 2014). In fact there is evidence in

songbirds that certain developmental stressors (notably undernutrition) negatively impact both the development of the song system in the brain (Buchanan, Leitner, Spencer, Goldsmith, & Catchpole, 2004; MacDonald, Kempster, Zanette, & MacDougall-Shackleton, 2006; Nowicki, Searcy, & Peters, 2002a; Spencer, Buchanan, Leitner, Goldsmith, & Catchpole, 2005) and attributes of song such as complexity and copy accuracy (Buchanan, Spencer, Goldsmith, & Catchpole, 2003; Nowicki et al., 2002a; Schmidt, Moore, MacDougall-Shackleton, & MacDougall-Shackleton, 2013; Spencer, Buchanan, Goldsmith, & Catchpole, 2003) while at the same time negatively affecting other cognitive abilities (Farrell et al., 2016; Farrell, Weaver, An, & MacDougall-Shackleton, 2012; Kriengwatana, Farrell, Aitken, Garcia, & MacDougall-Shackleton, 2015; Pravosudov, Lavenex, & Omanska, 2005). Even though associations of song learning ability and other cognitive abilities can be indirect in this fashion, testing for such associations is nevertheless relevant to the question of whether song learning is a separate cognitive module because the lack of such associations is difficult to reconcile with the hypothesis that song learning is a component of general intelligence. Accordingly we next review evidence on the association of song and cognitive abilities in general.

ASSOCIATIONS OF SONG AND COGNITIVE ABILITY

The first songbird in which the relationship of song to cognitive ability was examined was the zebra finch, a species in which males have a small repertoire of song elements (3–15) that are usually repeated in a single stereotyped sequence (Williams, 2004). Boogert, Giraldeau, and Lefebvre (2008) recorded 26 male zebra finches in captivity and measured three features related to song complexity: total number of elements per song, number of unique elements per song and song duration. One measure of cognitive ability was taken: the number of trials needed to master a novel foraging skill, one that required birds to remove a lid covering a well to obtain food. In a stepwise regression, the number of trials needed to solve the foraging problem was negatively related to the total number of song elements per song. Thus the association was in the predicted direction: learning performance was better in birds with more complex song (Table 1). In a later study of zebra finches, however, Templeton, Laland, and Boogert (2014) found no association between song complexity and success in learning a similar lid-flipping task, performed in this case in a social context, despite a larger sample of subjects ($N = 36$). This study also found no association between lid-flipping success and other song variables such as rate of production of unique elements and acoustic density (proportion of sound versus silence), nor between song complexity and latency to solve a barrier task, which required moving through a hole in a partition to reach food (Table 1).

The association of song and cognition has also been studied extensively in song sparrows. This species has song repertoires that vary in size geographically (Peters, Searcy, Beecher, & Nowicki, 2000), but which are almost always in the range of 5–13 song types. Boogert, Anderson, Peters, Searcy, and Nowicki (2011) recorded repertoires of free-living males and then tested them in captivity on a battery of four cognitive tests: the lid-flipping task, a colour association, a colour reversal and detour reaching. Song repertoire size in a moderate sample of subjects ($N = 22$) was significantly correlated in the expected direction with success on the detour-reaching test and in a larger sample ($N = 51$) was significantly correlated in the opposite direction with success on the colour reversal test (Table 1). There was no correlation between song repertoire size and success on the two remaining tests. In a second study of song sparrows, Sewall, Soha, Peters, and Nowicki (2013) found that, in a small sample ($N = 14$), spatial learning ability was negatively correlated with song

Table 1
Relationships of song features to cognitive abilities in songbirds

Species	Study	Cognitive tests	Song measures	Significant results
Zebra finch	Boogert et al. (2008)	Novel foraging problem	Total elements per song Unique elements per song Song phrase duration	Positive association of total elements per song and novel foraging ($N = 26$)
	Templeton et al. (2014)	Novel foraging problem Barrier task	Total elements per song Unique elements per song Song phrase duration	No associations found ($N = 36$)
Song sparrows	Boogert et al. (2011)	Novel foraging problem Colour association Colour reversal Detour reaching	Song type repertoire size	Positive association of detour reaching and song repertoire size ($N = 22$) Negative association of colour association and song repertoire size ($N = 51$)
	Sewall et al. (2013)	Spatial learning	Song repertoire size	Negative association of repertoire size and spatial learning ($N = 14$)
	Anderson et al. (2017)	Novel foraging Colour association Colour reversal Detour reaching Spatial learning	Proportion of notes copied from models Copy accuracy Song repertoire size	No associations found ($N = 19$)
Satin bowerbirds	Keagy et al. (2011)	Barrier removal Object covering Stick handling Building flexibility Templating	Mimetic repertoire size	No associations found ($N = 21$)
European starlings	Farrell et al. (2012)	Novel foraging problem Spatial memory	Song bout duration	Mean bout duration positively associated with spatial learning ($N = 19$)
Swamp sparrows	DuBois et al. (2018)	Novel foraging problem Colour association Colour reversal Detour reaching Spatial memory	Mean song typicality Maximum song typicality Mean vocal deviation Minimum vocal deviation Song repertoire size	No associations found ($N = 46-49$)

repertoire size, meaning that males with more complex song learned more slowly (Table 1).

In a third study of song sparrows, Anderson et al. (2017) measured song learning in hand-reared males ($N = 19$) that had been tutored with recorded song. Two measures of song learning were used: the proportion of a subject's notes that were copied from notes in the training songs (proportion copied) and the average spectrogram cross-correlation value between copied notes and model notes (copy accuracy). These are arguably more direct measures of song learning than are measures of song complexity. Five cognitive tests were administered, including the four used by Boogert et al. (2011) plus a spatial learning task. None of the five cognitive measures were significantly correlated with either proportion copied or copy accuracy, nor were they correlated with song repertoire size (Table 1).

Keagy et al. (2011) studied cognition and song in satin bowerbirds, a species that incorporates vocalizations learned from other species in their courtship songs (Loffredo & Borgia, 1986). Mimetic repertoire size, the number of other species copied by a male bowerbird, was the sole measure of song. The cognitive tests took advantage of the bower-building behaviour of the species, for example by measuring the success of bower owners in covering or removing unwanted objects placed on their bowers. In a sample of 21 males, Keagy et al. (2011) found no significant associations between mimetic repertoire size and any of their five cognitive measures (Table 1).

Farrell, Weaver, An, and MacDougall-Shackleton (2012) investigated the relationship between song and cognition in laboratory-reared European starlings. Males of this species possess repertoires of dozens of song types (Eens, Pinxten, & Verheyen, 1991). Farrell et al. (2012) found that starlings subjected to food restriction during their first 90 days posthatching later did worse than controls on a spatial foraging task but better on a novel foraging problem (which required removing a paper plug from a tube to access a food reward). Relative to food-restricted birds, controls produced longer song bouts, a trait that is positively associated with song repertoire size in starlings (Eens et al., 1991). From the present perspective, the most important results of this study were that mean bout duration was positively related to performance on the spatial task but was not correlated with success on the novel foraging problem (Table 1).

Finally, DuBois et al. (2018) examined associations between the song of male swamp sparrows recorded in the field and performance on a battery of cognitive tasks in the laboratory. The same test battery was used as in the Anderson et al. (2017) study of song sparrows, including tests of novel foraging, colour association, colour reversal, detour reaching and spatial memory. Swamp sparrows have small repertoires of two to five simple song types, usually consisting of a single syllable repeated in a steady rate trill (Ballentine, 2006). Lachlan, Anderson, Peters, Searcy, and Nowicki (2014) showed that the songs produced by a population of swamp sparrows can be clustered by acoustic measures, and that both male and female swamp sparrows respond more strongly to 'typical' songs that fall near the centroid of a cluster than to 'atypical' songs that fall farther from the centroid. Thus, typicality provides a measure of song quality that presumably reflects precision of song learning. DuBois et al. (2018) measured each male's mean typicality (averaged across song types) and maximum typicality (for each male's best song type), as well as song repertoire size and mean and minimum vocal deviation. These last two measures assess physical performance (Byers, Hebets, & Podos, 2010) rather than song learning. Sample sizes varied from 46 to 49 males (depending on the cognitive test). In linear mixed effects models controlling for neophobia, the five song measures were not associated with success on any of the five cognitive tests (Table 1).

Across the eight studies of five species summarized in Table 1, three cases were found in which a cognitive measure was significantly and positively associated with a song measure, meaning that better cognitive ability was associated with better song. Conversely, two cases were found in which better cognitive ability was

significantly associated with worse song. In the great majority of cases, pairwise associations between cognitive ability and song were not significantly different from 0. In two of the three cases of significant positive associations (one with zebra finches and one with song sparrows), subsequent investigation of the same variables in the same species found no association — in other words the result was not replicated. We conclude that song learning does not seem to be associated with general cognitive ability — or 'intelligence' — in songbirds, and perhaps not with any other specific cognitive abilities either. That conclusion is in accord with the view that song learning in songbirds is a primary cognitive module that has evolved separately from other cognitive abilities, and thus is not an aspect of general intelligence.

BIRDSONG LEARNING AND LANGUAGE DEVELOPMENT IN HUMANS

Human language learning has sometimes been viewed as being modularized (Fodor, 1983; Lenneberg, 1967), but there are substantial arguments against this interpretation (Fitch, 2010). Although there are areas of the human brain important to speech production and comprehension (Price, 2010), the speech control system is not as localized and highly structured as expected for a Fodorian module (Lieberman, 2002). Speech production and comprehension also do not appear to be computationally autonomous in the way Fodor (1983) expected for cognitive modules, instead relying heavily on general cognitive resources such as working memory (Baddeley, 2003). Most importantly, language learning is positively associated with other cognitive abilities, contrary to what has been found for birdsong learning. Measures of verbal ability correlate positively with other cognitive measures in humans as is true for human cognitive abilities in general (Carroll, 1993). Unlike song repertoire size in birds, vocabulary size in humans is positively correlated with other measures of intelligence (Lehrl, Triebig, & Fischer, 1995; Terman, Kohs, Chamberlain, Anderson, & Henry, 1918). Intriguingly, humans are able to judge the intelligence of others with some success using brief performances on verbal tasks such as reading headlines, making conversation, or (ironically) singing a song (Borkenau, Mauer, Riemann, Spinath, & Angleitner, 2004).

Despite this possible difference in modularization, we believe much can be learned about the evolution of language learning in humans from studying song development in songbirds. Aspects of birdsong development that are relevant include not only attributes of vocal production learning, such as its evolutionary origin and neural architecture, but also other forms of vocal learning, such as usage learning and comprehension learning. Below we outline the relevance of birdsong development to each of these aspects of human language development.

Origin of Vocal Production Learning

Songbirds provide the most diverse array of vocal learning species for use in generating and testing hypotheses on the origin of vocal production learning, which then can be applied to humans. Such hypotheses need to propose a selective benefit that would have been experienced by those signallers that first began to modify their vocalizations based on hearing the sounds of others; benefits experienced by receivers of the learned vocalizations or by the populations to which the signallers belonged are not relevant (Nowicki & Searcy, 2014). One long-standing hypothesis on the origin of song learning in songbirds is that learning from others allowed males to expand their song repertoires and hence benefit from female preferences for more complex song (Nottebohm, 1972; Nowicki & Searcy, 2014). In light of recent evidence that the

ancestral state in songbirds was for both sexes to sing (Odom, Hall, Riebel, Omland, & Langmore, 2014), this hypothesis may need to be modified by positing a benefit to repertoire expansion that would have been experienced by both sexes. Such an advantage is provided by the greater effectiveness of larger song repertoires in territory defence (Krebs, Ashcroft, & Webber, 1978; Yasukawa, 1981), coupled with the propensity of females as well as males to compete aggressively for resources (Rosvall, 2011; Tobias, Montgomerie, & Lyon, 2012). This hypothesis can be modified for application to humans, in whom vocal production learning may again have evolved due to selection for repertoire expansion (Nowicki & Searcy, 2014), with the benefits coming either through sexual selection by female choice (Darwin, 1871) or through kin selection for information sharing (Fitch, 2010).

Neural Architecture of Vocal Production Learning

Songbirds and humans exhibit similarities in the neural systems that control learning and production of song and language (Petkov & Jarvis, 2012; Prather, Okanoya, & Bolhuis, 2017). In particular, both groups possess a forebrain motor system for control of learned vocalizations that features a direct connection from the motor cortex to the motoneurons controlling the vocal organ (Nottebohm et al., 1976; Petkov & Jarvis, 2012). A similar direct connection seems to be lacking in at least some birds that are not vocal learners (Petkov & Jarvis, 2012). The appearance of such a direct connection is hypothesized to have been a key step in the evolution of vocal production learning in both songbirds and humans (Fitch, 2017; Jarvis, 2004), although recently it has been argued that a direct connection appeared substantially earlier in primate evolution than this hypothesis assumes (Lameria, 2017). Another parallel at the neural level is the lateralization of control that has been found for both human speech (Friederici, 2011) and birdsong (Nottebohm et al., 1976; Prather et al., 2017). Lateralization of language in humans has been used to support the idea that human language originated as gestural communication, given the lateralization of manual control in humans and to a lesser extent in apes (Corballis, 2012). Lateralization of song production in songbirds weakens this argument, however, as song is lateralized in this group but is unlikely to have evolved from gestures.

Vocal Interaction Learning

Vocal interaction learning is an aspect of vocal usage learning (Janik & Slater, 2000) in which individuals learn how to use their vocalizations to interact with others. In humans, the most common form of vocal interaction is conversation, which is thought to be the original and still the primary context for human language (Levinson & Torreira, 2015). Songbirds use their vocalizations in a variety of types of interactions, including countersinging, song type matching, repertoire matching and duetting. The development of the rules governing such vocal interactions is another area in which there are parallels between songbirds and humans (Rivera-Cáceres & Templeton, 2017) that can shed light on human language and its evolution.

Sacks, Schegloff, and Jefferson (1974) proposed that turn taking is a basic form of organization structuring human conversations, with rules mandating that, for the most part, only one individual speaks at a time and that speaker-change occurs efficiently, with offset times varying from a brief silent gap down to a very brief overlap. Mean offset times differ between languages but usually average around 200 ms (Roberts, Torreira, & Levinson, 2015; Stivers et al., 2009). Gaps of this magnitude are considerably shorter than the latencies required to initiate speech production (Levinson & Torreira, 2015), which implies that the next speaker must predict

the termination of the present speaker's turn and initiate speech before the present speaker stops talking. Offset times are longer in young children than in adults and decrease in children between ages 1 and 6 (Casillas, Bobb, & Clark, 2016), suggesting that turn-taking skills are learned.

In birds, the closest analogue to human turn taking occurs among species in which mated pairs perform antiphonal duets, meaning that the male and female sing alternate phrases within a song. The degree of temporal precision in such duets varies widely among species (Hall, 2009), but in some cases timing is even more precise than in human turn taking. In canebrake wrens, *Cantorchilus zeledoni*, for example, a male answers his mate with a mean gap of 46 ms while overlapping only 7% of her phrases across a mean of 19 different duet types per pair, while a female answers her mate with a mean gap of 64 ms while overlapping only 2% of his phrases (Rivera-Cáceres, 2015). Juveniles duet with their parents during the first months of life, and their behaviour provides evidence of learning that directly parallels the evidence in humans: the young birds overlap more of their duetting partner's phrases than do adults and their frequency of overlapping decreases with age (Rivera-Cáceres, Quiros-Guerrero, Araya-Salas, Templeton, & Searcy, 2018). Further evidence of learning is that a young bird copies the choices of phrase types used by its same-sex parent to answer each of the phrase types of its opposite-sex parent, a set of choices that is unique to each pair of parents. A juvenile's precision in using this pair-specific 'duet code' improves with age just as occurs with timing (Rivera-Cáceres et al., 2018).

Turn taking also occurs in common marmosets, *Callithrix jacchus*, in which the proper timing again seems to be learned (Chow, Mitchell, & Miller, 2015; Takahashi, Fenley, & Ghazanfar, 2016). Offset times, however, are an order of magnitude longer in marmosets (Takahashi, Narayanan, & Ghazanfar, 2013) than in humans and canebrake wrens, making the wrens in some respects a more satisfactory model for human interaction learning than are these monkeys.

Vocal Comprehension Learning

Vocal comprehension learning, in which an animal learns to extract new meaning from a signal based on experience (Janik & Slater, 2000), is another aspect of vocal communication in which songbirds show sophisticated cognitive abilities. Territorial songbirds, for example, can learn to discriminate neighbours from strangers based on song alone (Stoddard, 1996; Weeden & Falls, 1959), and in many instances can learn to recognize which individual neighbour each song represents (Falls, 1982; Falls & Brooks, 1975). These abilities apparently function regardless of the size of the song repertoire that must be recognized (Stoddard, 1996), and learned recognition can be retained from one year to the next (Goddard, 1991). Territory owners can use these recognition abilities to modulate their aggressive response to song based on the general aggressiveness of the singer (Hyman & Hughes, 2006) or on recent aggression shown by the singer to themselves (Akçay et al., 2009) or to neighbours (Akçay, Reed, Campbell, Templeton, & Beecher, 2010). These last instances are examples of what linguists refer to as pragmatics, which in its broad sense encompasses the context dependence of the interpretation of signals by receivers (Scott-Phillips, 2017). Communication via signals whose meanings are context dependent is arguably more complex cognitively than communication via referential signals whose meanings are relatively fixed, suggesting that pragmatics may play an especially important role in language evolution (Wheeler & Fischer, 2012). The importance of pragmatics in communication via birdsong thus provides another avenue by which investigation of birdsong can shed light on the evolution of language.

CONCLUSIONS

Song learning in songbirds is cognitively complex and the most language-like aspect of birdsong. Unlike language learning in humans, however, present evidence suggests that song learning in birds involves a separate cognitive module, not associated with other cognitive domains or with general intelligence (if such exists at all in birds). This conclusion derives from studies of song and cognitive abilities performed across several species of songbirds, which taken together show little evidence of consistent positive associations between song attributes and any cognitive ability. Song learning exhibits many of the attributes of a primary cognitive module as well, including domain specificity, computational autonomy, and a localized and highly structured neural architecture. Despite the conclusion that modularization is a likely point of dissimilarity between birdsong learning and language learning in humans, much can be learned about language learning from studying song learning, in particular concerning the selective benefits leading to the origin of vocal production learning, the nervous system modifications necessary for this origin, and the evolution of vocal interaction learning and vocal comprehension learning.

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