Twitter evolution: converging mechanisms in birdsong and human speech

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Abstract | Vocal imitation in human infants and in some orders of birds relies on auditory-guided motor learning during a sensitive period of development. It proceeds from 'babbling' (in humans) and 'subsong' (in birds) through distinct phases towards the full-fledged communication system. Language development and birdsong learning have parallels at the behavioural, neural and genetic levels. Different orders of birds have evolved networks of brain regions for song learning and production that have a surprisingly similar gross anatomy, with analogies to human cortical regions and basal ganglia. Comparisons between different songbird species and humans point towards both general and species-specific principles of vocal learning and have identified common neural and molecular substrates, including the forkhead box P2 (*FOXP2*) gene.

Charles Darwin famously suggested that there is "no fundamental difference between man and the higher mammals in their mental faculties"[1]. Although Darwin's claims have not remained unchallenged[2], his evolutionary principle of descent with modification has inspired much of the research into animal parallels to human speech and language. Vocal imitation, an important prerequisite for the evolution of spoken language (speech)[3,4], is shared with certain marine mammals, parrots, hummingbirds and songbirds[3–7], but seems to be absent in non-human primates[2,3]. Darwin himself had already noticed the parallels between language acquisition in human infants and song learning in birds[1]. From the 1960s onwards, birdsong researchers[5], more recently joined by biolinguists[8,9], have fleshed out his initial observations and discovered astonishing cognitive, neural and molecular parallels[7,10–13]. After addressing the behavioural similarities in vocal learning between humans and songbirds, we will focus on three important parallels. First, the architecture and connectivity of avian and mammalian brains are much more similar than had been recognized previously[14] (FIG. 1). For instance, avian pallial 'song' regions bear functional similarities with human auditory and motor cortices[15] and the importance of the basal ganglia for both speech and birdsong is starting to be understood mechanistically[16,17]. Second, recent insights from biolinguistic analyses comparing the structure of language and birdsong have also contributed new perspectives on the structure and perception of vocalizations[8,12,13], yielding hypotheses amenable to neurobiological analysis. Finally, the discovery that forkhead box protein P2 (FOXP2) is relevant for speech[18] led to experiments in songbirds that support the link of this gene to vocal learning[11,19,20]. We will review these developments, put them into an evolutionary context and discuss future prospects for the comparative analysis of birdsong, speech and language. Emerging common principles suggest that distant evolutionary lineages can evolve surprisingly similar behavioural, neural and molecular solutions for particular functions[2], as has been demonstrated previously for the evolution of vision[21] and locomotion[22].

FOXP2
A transcription factor of the large forkhead box (Fox) family, originally discovered in *Drosophila*. FOX genes have important roles in the development of many tissues and diseases.

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Vocal learning in birds and humans

There are striking parallels between the way infants learn to speak and birds learn to sing[5,10,23] (BOX 1), providing an experimental platform for investigating the brain mechanisms of auditory–vocal learning. First, in both cases, learning is the product of the interaction of predispositions and specific experience. If young songbirds are exposed to songs from their own and from another species, they will mainly imitate the conspecific song, although they are physically able to sing the heterospecific song[24]. The amazing ability of young children to acquire any one of more than 6,000 languages fluently without conscious effort or formal instruction suggests a predisposition for this complicated task[5,25]. However, the fact that children learn the language or languages to which they are exposed highlights the importance of experience in this process. Thus, both human infants and the young of many bird species acquire their speech and song repertoire, respectively, through a combination of predispositions and learning. However, what can be learned is constrained in both species by morphology and physiology. What sounds can be heard, remembered and imitated does not only depend on the brain regions that analyse, process and store auditory information and translate it into motor commands. The physical

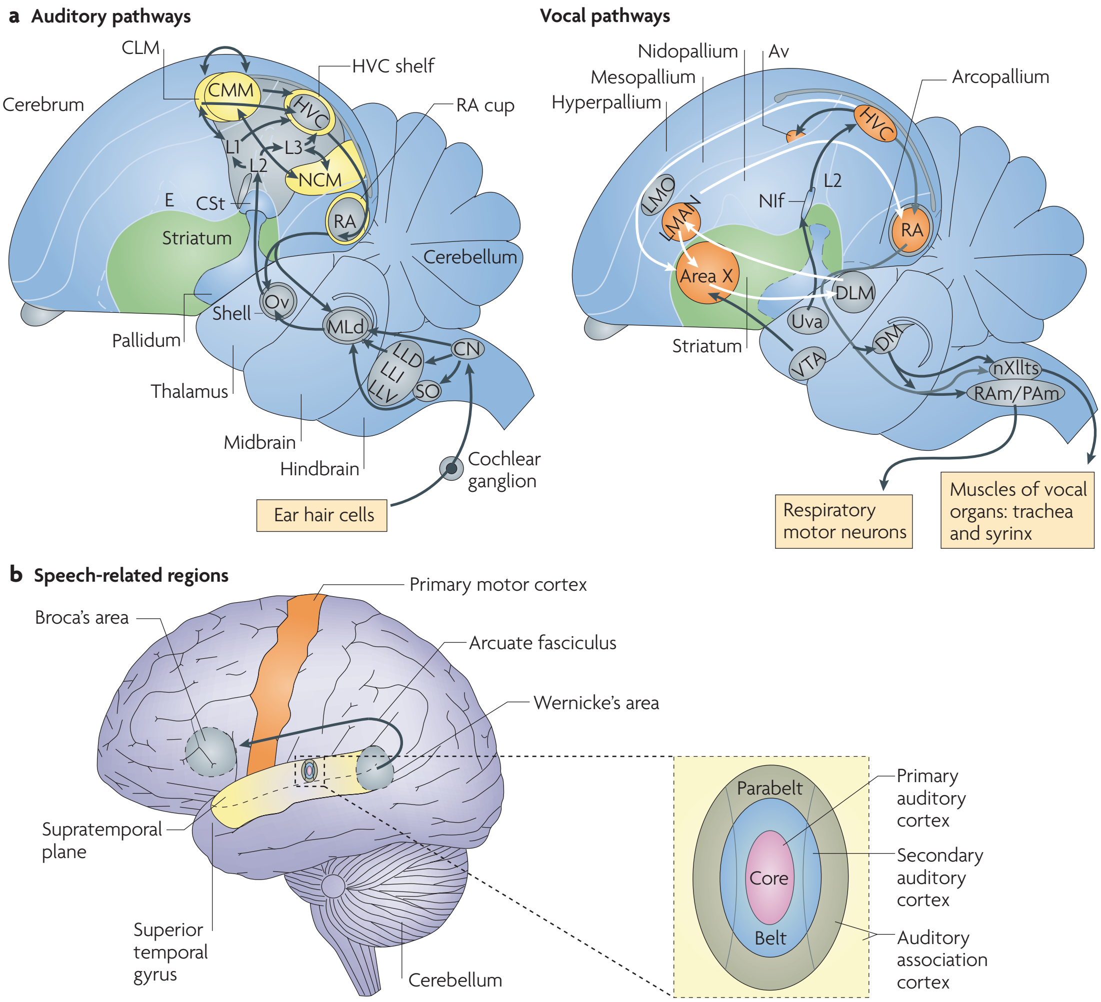


Figure 1 | **The songbird brain and the human brain. a** | Schematic diagram of a composite view of parasagittal sections of a songbird brain, giving approximate positions of nuclei and brain regions. Auditory pathways, with the known connections between the Field L complex, a primary auditory processing region and some other forebrain regions are shown (left panel). Brain regions that show increased neuronal activation when the bird hears song are represented in yellow. The caudomedial nidopallium (NCM) and caudomedial mesopallium (CMM) regions are thought to contain the neural substrate for tutor song memory[7,51–53,62]. Vocal motor pathways are also shown (right panel). Lesion studies in adult and young songbirds led to the distinction between a posterior pathway, known as the song motor pathway (SMP)[16] (shown by grey arrows), considered to be involved in the production of song, and a rostral pathway (shown by white arrows), known as the anterior forebrain pathway (AFP), that is thought to play a role in song acquisition and auditory–vocal feedback processing[6,7,16]. The two networks together are called the song system. The orange nuclei in the song system show substantially enhanced neuronal activation when the bird is singing. **b** | Schematic view of the left side of the human brain, showing regions that are involved in speech and language. Broca's area is particularly involved in (but not limited to) speech production, whereas Wernicke's area is involved in speech perception and recognition, as well as other language-related tasks. The two regions are connected by the arcuate fasciculus. Area X, Area X of the striatum; Av, avalanche; CLM, caudal lateral mesopallium; CN, cochlear nucleus; CSt, caudal striatum; DLM, dorsal lateral nucleus of the medial thalamus; DM, dorsal medial nucleus of the thalamus; E, entopallium; L1, L2, L3, subdivisions of Field L; LLD, lateral lemniscus, dorsal nucleus; LLI, lateral lemniscus, intermediate nucleus; LLV, lateral lemniscus, ventral nucleus; LMAN, lateral magnocellular nucleus of the anterior nidopallium; LMO, lateral oval nucleus of the mesopallium; MLd, dorsal lateral nucleus of the mesencephalon; NIf, interfacial nucleus of the nidopallium; nXIIts, tracheosyringeal portion of the nucleus hypoglossus (nucleus XII); Ov, ovoidalis; PAm, para-ambiguus; RA, robust nucleus of the arcopallium; RAm, retroambiguus; SO, superior olive; Uva, nucleus uvaeformis; VTA, ventral tegmental area. Part **a** is modified, with permission, from REF. 15 © (2005) Macmillan Publishers Ltd. All rights reserved.

Seasonal breeder
An animal (for example, a songbird species) that breeds only during a specific period of the year.

Opportunistic breeder
An animal (for example, a songbird species) that can breed year-round.

Action-based learning
Also known as selective learning. A song learning style that selects the final sound repertoire after an initial overproduction of song elements, based on auditory or visual feedback from conspecifics.

Instruction-based learning
Also known as sensorimotor learning. A song learning style principally exemplified by the zebra finch, in which vocal 'babbling' is gradually modified through auditory guided sensorimotor learning. Both 'instruction-based' and 'action-based' learning can occur in the same species to various degrees.

properties and function of the ear, the sound source (the larynx in humans, the syrinx in birds) and the vocal tract also play an important part[26].

The interaction between 'innate' predispositions and specific experience is evident when songbirds are reared in isolation. Without exposure to tutor song, isolates sing highly abnormal, so-called 'isolate song'. However, a predisposition is also evident, because isolate song retains certain species-specific features[27,28]. Strikingly, when young zebra finches (*Taeniopygia guttata*) were tutored with a song from an isolate conspecific, they produced a fairly accurate imitation but also spontaneously improved the abnormal song towards more species-typical features[29]. Using this slightly improved song to tutor a new generation of young finches the authors found that with each generation, song more closely resembled — and was eventually indistinguishable from — typical zebra finch song. These findings demonstrate that the neural substrates for learned vocalizations can apparently carry quite exact pre-specifications for particular acoustic features and an overall acoustic 'gestalt', yet allow a high degree of plasticity for what can be learned within those constraints. Indeed, these data echo (controversial) claims about the spontaneous emergence of grammatically correct language in children that have been exposed to agrammatical 'creole' language[25].

Second, in both humans[5,30] and songbirds[5,6,28], there is a phase early in development when auditory–vocal learning is accomplished best, called the 'sensitive period'. In humans, learning new languages without formal instruction becomes increasingly less effective after puberty, and adults have difficulty speaking foreign languages without an accent[30]. To what extent songs continue to change in adulthood varies greatly among different bird species[31]. This species variability is useful in dissecting the neural mechanisms underlying adult song plasticity[32].

Third, in young humans and in juvenile birds of many species a listening phase precedes a production phase. When speech- (or song-) production starts, both humans and songbirds produce vocalizations that are quite different from those of adult conspecifics. During well-defined stages, starting with 'babbling' in human infants and 'subsong' in songbirds, their vocalizations gradually come to resemble the adult form[5]. Different bird species vary considerably with respect to learning strategies during song development[33]. The period during which song auditory memory is formed, the 'auditory memorization phase' (BOX 1; Supplementary information S1 (box)) can precede the period of learning to sing songs (sensorimotor learning) by months[34]. This is the case for many seasonal breeders, such as the white-crowned sparrow (*Zonotrichia leucophrys*). Similarly, in humans, auditory learning and understanding language precede language production. By contrast, in opportunistic breeders, such as the zebra finch, auditory and motor learning overlap[35]. How much and when the developing song is shaped by auditory experience also varies considerably among bird species. Unlike children, some songbird species can develop their entire species-typical adult repertoire of song elements without exposure to conspecifics, but which elements constitute the final song is strongly influenced by what neighbours are singing ('action-based learning')[33,36]. In others, 'innately' produced sounds are continually adjusted towards a memorized tutor song throughout development ('instruction-based learning')[33,37]. Cumulative evidence suggests that the relative contribution of experience-independent versus experience-dependent developmental song production can be linked to different brain pathways[38] (see below; FIG. 1; Supplementary information S2 (box)). In humans, patients that have sustained damage to certain parts of the cortex can lose speech while they retain emotional vocalizations such as sobbing, crying and laughing[39]. Although speech requires specialized cortical regions, these emotional vocalizations seem to be controlled by subcortical structures[40].

Fourth, in both humans and songbirds vocal learning is enhanced by social interaction with the 'tutor' (REFS 41,42) and in birds it can even be influenced by feedback from non-singing females[43].

These remarkable similarities between speech acquisition and birdsong learning have, over the last 10 years, been extended to the neural and genetic levels. Birdsong provides a formidable model paradigm to investigate neural and molecular mechanisms of auditory–vocal learning experimentally, at the cellular and subcellular levels, mechanisms that are not amenable to study in human infants. Furthermore, recent research has suggested the possibility of parallels at the level of syntax (BOX 2; Supplementary information S3 (box); Supplementary information S4 (box)). Below, we discuss the most important evidence for parallel mechanisms at all of these levels, as well as the important implications of this evidence for our understanding of the evolution of brain and cognition.

Box 1 | How songbirds learn to sing and human infants learn to speak

Song learning in birds and speech learning in humans entails the imitation of species-specific communication sounds[5–7,28] (Supplementary information S1 (box)). Young songbirds (usually males) learn their song from an adult male tutor. In many songbird species, such as the zebra finch, song learning has two phases: a memorization phase, during which the tutor song is stored in long-term memory, and a sensorimotor phase during which the bird's own vocal output is 'matched' with the memorized information. The mechanism underlying song memorization has been called a 'template' (REF. 27), which is essentially the central representation of song.

Whether a universal template for human language exists and if so, what its nature is, is the subject of intense linguistic debate. At one end of the spectrum, it is argued that all languages share core grammatical rules that reflect language-specific innate dispositions and neural computations that are unique to language[3,45]. At the other end of the spectrum, it is argued that grammatical diversity among languages far outstrips the similarities, and that the general-purpose learning capacity of the human brain is sufficient to explain language learning[134].

Human speech sounds are constrained by our vocal apparatus and certain sound combinations are more biologically feasible than others. These 'phonetic universals', for example, certain sound combinations that tend to be found in all languages, are akin to what songbird researchers might call a 'template for species-specific syllables'. When a young songbird starts to sing during the sensorimotor phase, its song output is not yet stereotyped and does not resemble the tutor song very well. This kind of vocalization is known as 'subsong' (REF. 28). The production of subsong is reminiscent of 'babbling' in human infants[5,41]. During the sensorimotor phase the bird is thought to match its own output with the refined template, and, after the so-called 'plastic song' phase, it eventually produces what is known as crystallized song.

Syntax
In a narrow sense, syntax refers to a set of rules that governs the arrangements of words to produce a sentence. In a broader sense, syntax refers to a set of rules to hierarchically and sequentially arrange elements to produce a string.

Song system
A network of forebrain nuclei that is involved in the perception, acquisition and production of song.

Components of birdsong and human language

Similarities between human speech and birdsong notwithstanding, many authors have emphasized the important differences between them. Perhaps most strikingly, in natural languages, distinct word orders and combinations are associated with distinct sentence meanings, for which no adequate analogues have so far been demonstrated in songbirds, or indeed in any non-human animals (Supplementary information S3 (box)). Some therefore doubt that any animal model can shed light on the nature and genesis of human language. Although language may indeed have a unique cognitive architecture[44], language has evolved in a biological substrate that is largely shared with other animals[3], making it plausible that certain aspects of human language can be studied through animal models[13]. In that case, to properly compare human language to the structured vocalizations of other animals we need to define meaningful levels of comparison.

Language pairs sounds with meanings. This requires a sensorimotor system that deals with the perception and production of speech sounds or gestures, and a meaning system that deals with reasoning and inference. The linguistic domain of grammar mediates between these two systems[3] (Supplementary information S3 (box)). It is generally thought that the uniqueness of human language consists of a computational system of grammar that translates meaning into a sequence of symbols, but considerable debate remains over the details of this system[3,45,46]. By contrast, comparisons between language and birdsong along the sensorimotor dimension have revealed parallels at both the neural, developmental–behavioural and genetic levels. We propose that the study of structure in animal vocalizations could also provide insights into the structural properties of human language, even though the intimate relationship between structure and meaning that exists in human language is thought not to exist in other animals[47] (Supplementary information S3 (box); S4 (box); S5 (box)).

The fact that such similar details of vocal learning arose in distinct evolutionary branches that parted ways some 300 million years ago[48] underscores that evolutionary selection pressure can result not only in similar morphological adaptations but also in similar behavioural adaptations. Whether or not these similarities are the consequences of convergent neural architecture and information processing is one of the major challenges facing neurobiologists who study birdsong and human speech from an evolutionary perspective (BOX 3).

Brains for birds and brats

Songbirds have specialized, discrete brain regions for song recognition, production and learning. Roughly, birdsong involves three interconnected neural networks[6,7,16] (FIG. 1a): first, secondary auditory regions — including the caudomedial nidopallium (NCM) and caudomedial mesopallium (CMM) — are involved in song perception and are important for the recognition of tutor song[7]; second, the song motor pathway (SMP)[16] — a posterior motor pathway connecting the HVC, the robust nucleus of the arcopallium (RA) and the tracheosyringeal portion of the nucleus hypoglossus (nXIIts) — is involved in song production and certain aspects of song learning[6,49]; and third, the anterior forebrain pathway (AFP)[6,17] — an anterior cortical–basal ganglia–thalamic loop that originates in the HVC and passes through Area X (part of the avian basal ganglia[6]), the thalamic nucleus dorsolateralis anterior pars medialis (DLM) and the lateral magnocellular nucleus of the anterior nidopallium (LMAN), and eventually connects with the motor pathway at the nucleus RA — is essential for sensorimotor learning and adult song plasticity (FIG. 1a). The second and third pathways (the SMP and AFP) together are usually called the 'song system' (REF. 7).

In the zebra finch, the NCM and the CMM are involved in auditory memory[7]. It has been suggested that the NCM contains the neural substrate of the memory of songs and calls[50]. Indeed, neuronal activation in the NCM of adult zebra finch males in response to tutor song correlates with the strength of song learning (measured as the number of song elements copied from the tutor song).[51–54]

The behavioural similarities between birdsong learning and speech acquisition raise the issue of whether the brain organization of auditory–vocal representation is similar in songbirds and humans. At face value, this would seem unlikely, as human and songbird brains are of different size and gross morphology (FIG. 1). In human adults, the neural substrate of motor representations of speech is traditionally thought to involve regions in the inferior frontal cortex (including Broca's area)[55], whereas perception and memory of speech is considered to involve regions in the superior temporal

Box 2 | Neural mechanisms of birdsong 'syntax'

Human speech and birdsong both consist of sequentially arranged utterances, and the motor and perceptual mechanisms that enable such sequencing might be similar between birds and humans. The neural mechanisms of human syntax are briefly discussed in Supplementary information S4 (box). As we do not know whether birdsong has syntax in the same sense in which the concept is applied to human language, we limit our discussion to the mechanisms by which song sequences are produced and perceived.

Depending on the social context, song sequences can vary. For instance, notes are sung in a much more linear way during courtship song in zebra finches than when the male sings by himself. Thus, a source of variability is required that controls which of various possible syllable combinations are chosen each time the bird sings. In zebra finches lateral magnocellular nucleus of the anterior nidopallium (LMAN) lesions eliminate song sequence variability[135], and differences in sequence variability associated with different social contexts correlate with the variability of spike timing in the LMAN neurons[136], suggesting that the source of variability may originate in the LMAN or upstream of the LMAN in the anterior forebrain pathway (AFP). In male zebra finches, HVC neurons that project to the robust nucleus of the arcopallium (RA) spike in short bursts precisely only at one particular time during a song sequence[137,138]. Some HVC neurons respond selectively to particular combinations of song elements[139] but there is also evidence that song auditory sequences are loosely coded by populations of HVC neurons[140]. These findings suggest that the HVC also has a role in song sequence generation.

Sequential processing of heard vocalizations in birdsong and syntax in human language (Supplementary information S4 (box)) involve forebrain regions, including motor regions (which are also important in the production of sequential signals). In both human speech and birdsong, when the auditory input becomes complex, the motor system is likely to become involved in the analysis of the vocalizations[81]. Research into sensorimotor integration and mirror systems (Supplementary information S6 (box)) will enable more specific comparisons of the neural mechanisms underlying birdsong and human speech.

Box 3 | A proposal for the evolution of auditory–vocal learning

There is increasing evidence for brain homologies between birds and mammals[15,57,58]. However, the capability for auditory–vocal learning in humans, certain bird species and marine mammals does not seem to be the sole result of common ancestry. Rather, the evidence suggests that there has been evolutionary convergence of the capability for auditory–vocal learning[2,3], whereby similar selection pressures were involved in distantly related taxa to solve similar problems[2]. To achieve auditory–vocal learning, humans and songbirds use analogous — and possibly homologous[15,57,58] — brain regions. Thus, an evolutionary scenario emerges in which there is both homology and convergence.

An influential proposal[3] regarding the evolutionary origin of language assumes that humans might have uniquely evolved a cognitive module for recursion (Supplementary information S5 (box)). We propose an alternative interpretation based on our comparative review of human speech and birdsong: the human ability to use recursion may be the result of interactions between simpler mechanisms that can also be identified in songbirds[13]. Specifically, vocal learning may have promoted an increase in the number of song elements, and the ability to alter the sequence of these song elements would further increase song variation. Both of these mechanisms may have evolved through sexual selection for song complexity[12]. A cognitive module for recursion might have evolved out of an interaction between this faculty of sequential manipulation and a general faculty of working memory. Working memory enables a bird to remember a song segment while it is singing subsequent segments of the song, and the bird could 'attach' the remembered part of the segment after it finishes singing the current part. Elaboration of this mechanism will allow embedding of a song segment into other parts of song segments, and eventually lead to a recursive song structure[13] (Supplementary information S5 (box)).

cortex (Wernicke's area and surrounding regions; FIG. 1b)[56]. However, despite the substantial differences between avian and mammalian brains, there are many analogies and homologies that have recently prompted a complete revision of the nomenclature of the avian brain[14,15]. A number of neuroanatomists[15,57,58] have suggested that the pallium (including the hyperpallium, mesopallium, nidopallium and arcopallium; FIG. 1a) is homologous with the mammalian neocortex. This view is not universally accepted[15], but a case has been made for similarities in connectivity and function that would suggest at least analogies between the human cortex and the avian pallium[7]. Within the avian pallium, Field L2 receives auditory connections from the thalamus and in turn projects onto Fields L1 and L3 (FIG. 1a). These two regions project to the caudal mesopallium and caudal nidopallium, respectively. Thus, if the avian pallium is homologous with the mammalian neocortex[15,57,58], it is plausible that the Field L complex is homologous with the primary auditory cortex in the mammalian superior temporal gyrus[7]. Interestingly, the primary auditory cortex in mammals also consists of three different 'core' regions that receive inputs from the thalamus. Extending the parallel[7], the projection regions of the Field L complex — the NCM and the CMM — are analogous with the mammalian auditory association cortex, in particular with belt and parabelt regions. Finally, the AFP loop in the song system (FIG. 1a) bears strong similarities in connectivity, neurochemistry and neuron types to the mammalian basal ganglia[17], and both the LMAN[59] and the HVC[5,60] have been tentatively suggested to correspond functionally to Broca's area.

It is important to note that the functional distinction between the temporal and frontal cortices in human speech is not as strict as was previously assumed[7,61,62]. In addition, there is continual interaction between these two cortical regions already in young children[7,61,62]. As we shall see, there is a similar kind of interaction between regions in the song system and the caudomedial pallium that are involved in auditory–vocal learning in songbirds[7,62].

Neural dissociation between song recognition and production. It has been proposed[7] that regions in the caudomedial pallium (including the NCM) contain the neural representation of tutor song memory that juveniles acquire, whereas nuclei in the song system are required for sensorimotor learning and song production[49]. In the white-crowned sparrow, a species in which the memorization and sensorimotor phases (BOX 1) of vocal learning do not overlap temporally, HVC neurons of juvenile males did not preferentially respond to songs with which they were tutored during the memorization phase (compared to other songs)[63]. Instead, the neurons preferentially responded to the bird's own song (BOS) — even when compared to tutor song[63] — when the males started to sing. In male zebra finches, in which memorization and sensorimotor phases overlap, HVC neurons initially responded preferentially to the tutor song, but during the second half of the sensorimotor phase and in adult zebra finches these neurons showed a preference for the BOS[64]. These findings suggest that the HVC is important for song production in the plastic song phase and that during this phase neurons in the HVC acquire their preferential responsiveness to the BOS.

In adult zebra finch males, lesions to the NCM impair recognition of the tutor song but do not affect song production[62] (FIG. 2). This suggests that in adult songbirds, access to a representation of tutor song memory (the 'template') is not necessary for the production of a song that was learned from the tutor. By contrast, lesions to the HVC in starlings disrupted song production but not recognition[65], and in adult male canaries lesions to the HVC and RA disrupted song production, whereas large lesions to the nidopallium and mesopallium did not[66]. Taken together, these studies reveal a 'double dissociation' (REF. 62) of the effects of lesions to the song system and to the NCM on song. In addition, juvenile zebra finch males that are still in the process of learning their songs show increased neuronal activation (measured as expression of the immediate early gene product ZENK) in response to conspecific song (compared to silence) in

Working memory
A form of memory in which information is stored for a limited period during which it can be used; in humans the classic example is remembering a telephone number that is then dialled and immediately forgotten.

Homologous
Homologous traits (or brain regions) are thought to have evolved from a common ancestor.

Analogous
Analogous traits (or brain regions) have a similar function, but are thought to have evolved independently in distantly related species.

Template
A term used to denote the central representation of birdsong. It is thought that songbirds are born with a crude template that has species-specific characteristics. Auditory experience, first with the song of an adult conspecific male and later with the individual's own vocal output, then moulds the template into a more precise representation of the tutor song.

the NCM and CMM but not in the song system nuclei HVC or RA[67]. Moreover, in the NCM, neuronal activation was greater in response to tutor song than to novel song[67]. Together, these findings suggest that there is a neural dissociation between song recognition and song production that is already apparent in juveniles[67].

The results of a number of studies suggest that the NCM is unlikely to contain the neural substrate for a representation of the BOS[7,53,62], but growing evidence indicates that such a representation may be subserved by the song system. A representation of the BOS might be what Nottebohm[68] called a 'motor program' that enables songbirds to produce their own song without access to the template. Electrophysiological analysis in adult zebra finch males showed that, overall, neurons in the song system nuclei HVC, RA, LMAN and Area X responded more strongly to the BOS than to the tutor song[69,70] or to the song of another conspecific[71]. Some neurons in the LMAN and Area X respond to the BOS and tutor song, whereas a small proportion of neurons in these nuclei respond more strongly to the tutor song[69]. Lesions to the Area X in adult male zebra finches did not affect the discrimination between conspecific or heterospecific songs in an operant conditioning paradigm, but such lesions did impair the ability to discriminate between the BOS and the songs of other zebra finches[72]. In addition, the expression of the immediate early gene *ZENK* in the HVC in adult zebra finch males exposed to the BOS (but not in adult males exposed to the tutor song or to a novel song) correlated with the strength of song learning during development[73]. Together with the electrophysiological evidence showing preferential responding to the BOS in the HVC[63,64,69], these findings suggest that in adult zebra finches the AFP contains a distributed neural representation of the BOS.

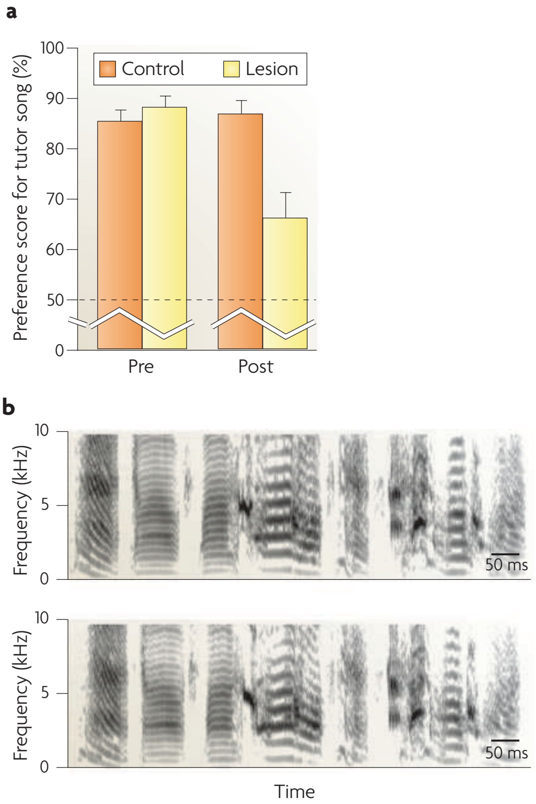


Figure 2 | **Neural dissociation between birdsong recognition and production. a** | Lesions to the caudomedial nidopallium (NCM) impair song recognition in zebra finch males. Song preferences were measured by calculating the amount of time spent near a speaker that broadcast the song of the bird's tutor compared to a speaker that broadcast a novel zebra finch song. Before surgery ('Pre'), birds in both groups showed a strong, significant preference for the song of the tutor over a novel song. After surgery ('Post'), birds in the sham-operated group had maintained their preference, whereas this was significantly impaired in the group that received lesions to the NCM. **b** | Representative spectrograms of a bird's song before surgery (top panel) and after surgery with lesions to the NCM (bottom panel), illustrating that song production was not altered by lesions to the NCM. Figure is reproduced, with permission, from REF. 62 © 2007 Cell Press.

Neural dissociation of speech perception and production in humans. A similar dissociation between brain regions involved in auditory perception and memory on the one hand, and vocal production on the other, exists in the case of human speech. Human newborns show increased activity (measured with magnetoencephalography) in the superior temporal lobe, but not in the inferior frontal cortex[74], in response to human speech. A functional MRI study in 3-month-old infants (which are in the 'cooing' stage of babbling in which syllables are not yet produced) showed activation in the superior temporal cortex as well as in Broca's area in the inferior frontal cortex in response to hearing speech[61]. The activation in Broca's area was specific for speech repetition, suggesting a possible role for Broca's area in auditory memory in pre-verbal infants. Six- and twelve-month-old infants exhibited increased activation (compared to baseline) in the superior temporal cortex and in the inferior frontal cortex when exposed to speech sounds[74]. Together, these studies suggest that the superior temporal cortex is — or is part of — the neural substrate for speech perception in neonates and that Broca's area becomes active at a later stage, when infants start babbling.

Auditory–motor interactions and error correction in birdsong and speech. In order to successfully imitate song or speech, the brains of songbird and human young have to solve the same problems. The motor system for speech and birdsong production must be appropriately controlled, vocal production must be compared to an auditory memory or template, and, if sound production does not match the auditory template, the error must be detected and the vocal signals must be changed accordingly. Thus, during both birdsong[49,75] and speech[76] learning, and to a lesser degree also in adulthood[49], vocal motor output must be monitored continually through auditory feedback and if errors are detected the output should be adjusted. How, where and when this happens have been central themes in songbird research and recent progress can provide testable hypotheses for speech research as well.

In songbirds, song-specific auditory information is thought to enter the song system at the level of the HVC from a small nucleus known as the interfacial nucleus of the nidopallium (NIf) and from higher auditory regions, notably the caudolateral mesopallium (CLM; see FIG. 1a)[77–80]. Preferential responsiveness to playback of species-specific songs is found throughout the song system[69–71], even in the hypoglossal motor nucleus innervating the syrinx[81]. Similarly, the human vocal motor system is sensitive to speech sounds. In human adults speech perception modulates the excitability of tongue muscles in a phoneme-specific way[82], and in human infants Broca's area is activated by speech from the babbling stage onwards[61,74]. The auditory sensitivity of the vocal motor system might be useful for the real-time modulation of own vocalizations and in the off-line evaluation of others' vocalizations. In the former, the auditory response in the motor system may be compared with the efference copy of the motor activity to evaluate vocal output. In the latter, auditory input may be evaluated in reference to the animal's own vocalizations.

Because lesions to nuclei in the AFP were found to have stronger effects on song during development than in adulthood[83–85], the 'AFP comparison hypothesis'[86] postulated the AFP to be involved in comparing auditory feedback with the tutor song memory. The outcome of this comparison was expected to influence the motor system at the level of RA, where the AFP and motor pathway converge[6] (FIG. 1a). Studies showing auditory responsiveness throughout the AFP in anaesthetized, sleeping and awake birds supported this idea[71,87–91]. Curiously, when the bird sings, auditory input does not seem to influence AFP activity[92], contradicting the idea that auditory feedback is evaluated on-line in the AFP. Rather, it suggests that the evaluation of auditory feedback might take place outside this pathway[92]. Potential locations could be the HVC–Area X projection neurons, the dopaminergic ventral tegmental area (VTA)–substantia nigra complex[93], which project to Area X, or the CLM[94]. What, then, is the role of the AFP? From the early lesion studies[83,84] it was clear that the AFP at minimum has to be functional for song plasticity, be it naturally occurring plasticity during song development or song plasticity experimentally induced in adult birds by altering auditory feedback through a variety of means (transsection of the syringeal nerves, deafening, manipulating individual notes by masking them with noise or altering their pitch)[49,75,95,96]. In addition to a 'permissive' role, an 'instructive' role for the AFP had long been postulated[83,84]. This led to the formulation of an 'error-correction hypothesis' for the AFP[49] that was based on the postulated role of vertebrate basal ganglia circuits in reinforcement learning[97]. Essentially, the error correction model assumes that the basal ganglia are involved in calculating the difference between the desired outcome and the actual performance, and outputs the difference as an 'error' signal. Recent studies have provided direct evidence for such an instructive role of the AFP. Particularly, when the auditory feedback of an individual note is experimentally manipulated while the bird sings the bird's brain seems to interpret the manipulated feedback as 'vocal errors' and it 'corrects' the 'errors' within hours by singing the note in question in a different manner[96,98,99]. Transiently inactivating the LMAN pharmacologically resulted in a rapid return to the note sung before auditory feedback manipulation[99], indicating that the LMAN has a role in this type of adjustment learning.

Manipulation of auditory feedback has also been used in the study of human speech, and brain imaging studies have started to reveal the neural mechanisms for real-time speech production[100]. When overt speech was masked by noise, activity in the insula and the anterior cingulate cortex increased, suggesting that these regions might be involved in speech adjustment. The anterior cingulate cortex has been implicated in error monitoring and evaluation[101] and receives direct and indirect projections from the basal ganglia[101], suggesting that functionally and anatomically the human anterior cingulate may be comparable with the songbird LMAN[60]. Taken together, accumulating evidence suggests that human speech and birdsong may be maintained and perhaps also learned in a functionally and neurally similar way: vocal motor regions are involved both in the production of vocalizations and in auditory perception, and auditory feedback is crucial for the maintenance of learned vocalizations, providing the basis for an error correction mechanism that influences the motor system.

In summary, evidence reviewed in the previous two sections suggests that in both human infants and songbirds there is a functional dissociation between brain regions mainly involved in auditory perception and memory, and brain regions involved in vocal production. The present section suggests that in both cases the functional dissociation is not absolute; for example, the 'vocal production regions' of the brain also have perceptual characteristics (BOX 2) that develop early in life. A picture emerges of a dynamic system of continually interacting brain regions involved in auditory–vocal learning as well as in vocal performance in adulthood.

FOXP2: a genetic toehold for song and speech

Human speech and birdsong are the result of a complex interaction between genetic and environmental influences[29,102]. However, little is known about which genes might be particularly relevant for these behaviours. Genetic manipulation studies and genome information regarding songbirds have only recently become available (see the NCBI Zebra Finch Genome Resources website), so that knowledge about genetic contributions to birdsong has lagged behind knowledge about the anatomical and physiological underpinnings of song production. In addition, finding genes that are involved in learned vocalizations is difficult, for the same reasons that hamper efforts to link genes to any behavioural trait (BOX 4). Nevertheless, mutations in the gene encoding the transcription factor FOXP2 have been found to be associated quite specifically with a speech disorder called developmental verbal dyspraxia (DVD) in a large three-generation family (the 'KE-family') and in some unrelated individuals[18,19]. All human *FOXP2* mutations identified so far are heterozygous and reduce the amount of functional FOXP2 by about half. Patients with DVD have difficulty in planning and producing the precise and specific series of movements of the tongue, lips, jaw and palate that are necessary for correct speech, but receptive linguistic processing can also be affected. Interestingly, sequence variants in the gene encoding contactin-associated protein-like 2 (*CNTNAP2)*, which is regulated by FOXP2, also segregate with language abnormalities[103,104]. The connection between *FOXP2* mutations and a speech deficit has provided a molecular toehold into pathways and mechanisms that underlie speech and language, and research on FOXP2 has since followed three main avenues. First, refining the speech phenotype and identifying neural structural and functional correlates in people with *FOXP2* mutations; second, analysing evolutionary changes in the *FOXP2* sequence across the animal kingdom and particularly in the hominin lineage; and third, using cell culture and animal models to gain insight into the mechanism of its molecular, cellular and behavioural actions. Below, we highlight recent findings concerning FOXP2 in songbirds that relate to the language phenotype in humans. For a more comprehensive review of FOXP2 research in other animals and *in vitro* model systems, sequence evolution and analysis of the human phenotypes, see REFS 19,103,105,106.

The *FOXP2* gene belongs to the large forkheadbox transcription factor family of genes that are highly evolutionarily conserved and implicated in many diseases and in developmental processes of many tissues[107]. Consistent with a developmental role of other Fox proteins, *FOXP2* is expressed in regions of the vertebrate embryo in which inductive signals organize adjacent proliferation of neural progenitors and subsequent migration[11]. *FOXP2* expression persists in adult avian — but not mammalian — brain regions where new neurons are born in adult brains[108]. Structural and functional brain imaging of humans with *FOXP2* mutations shows subtle volume differences and striking activation differences during language tasks, particularly in corticocerebellar and corticostriatal circuits[105]. Although these circuits were traditionally considered less important to speech than cortical language regions, there is now considerable evidence that they play important parts in motor functions and auditory processing related to speech[109]. In songbirds, the importance of the corticostriatal AFP circuit in song learning is underscored by a large body of data (see above), but information about the connectivity of the cerebellum with the song system and its role in singing behaviour is still sparse[110].

In summary, *FOXP2* expression studies in avian and mammalian embryos are consistent with a role for FOXP2 in early brain development of these pathways. This does not rule out the possibility that FOXP2 continues to have a role later in life. Indeed, *FOXP2* expression persists in the striatum, dorsal thalamus, cerebellum and other brain regions of adult birds and rodents[19], and there is clear evidence in adult songbirds that *FOXP2* is downregulated as a result of singing activity on a timescale of minutes to hours[111,112], as discussed below.

Semantics
In a narrow sense, semantics refers to the study of meaning in language. In a broader sense, semantics refers to information content of a signal.

Box 4 | **Genes and language**

Language is a polygenic trait — it requires many genes acting together at different levels. Because of the large dimensionality of biological systems involved in language, it is unlikely that particular genes will be exclusively associated with particular linguistic categories, for example, syntax or semantics. Genes important for language are also likely to be pleiotropic; a gene can be specifically linked to language (for example, be required for sensorimotor integration in a circuit dedicated to speech) but need not be uniquely associated with this trait — the same gene could have a different function in, for example, the immune system or the cardiovascular system.

Because language is likely to be subserved by large gene networks the effect of mutations in individual genes might not become apparent; large gene networks are robust against disturbance by malfunction of just one gene. In addition to searching for more multi-generation families like the 'KE family' in which the FOXP2 mutation was originally found to be inherited in a Mendelian form[18], genetic linkage and association analyses in human cohorts or quantitative trait mapping in birds can reveal genes related to language or birdsong, respectively. However, in order for statistical tests to have sufficient power, large experimental cohorts with well-defined behavioural phenotypes are required and these are difficult to obtain, both in humans and in birds.

FoxP2 and vocal plasticity. Research in songbirds has addressed the question of whether FOXP2 plays a role in neural circuits relevant for auditory-guided vocal motor learning. Considering the findings that implicate the AFP circuit in song development, it is interesting that in juvenile zebra finches, *FOXP2* mRNA expression levels in Area X are 10–20% higher than in the surrounding striatum during vocal sensorimotor learning[112,113]. This may be related to the fine-tuning of synaptic connectivity, because at this time neurons in the AFP have established synapses and are functioning, but the topography for this pathway still undergoes remodelling[114], and new neurons continue to be added to Area X throughout life[108].

A second correlation between FOXP2 levels and song plasticity exists in a strain of adult canaries that incorporate new song elements into their repertoire at the end of the breeding season. *FOXP2* expression in Area X is higher during this period than during the months when song is highly stereotyped[113]. A third link between vocal plasticity and *FOXP2* expression is provided by the fact that *FOXP2* expression levels are downregulated in Area X as a result of singing activity on a timescale of minutes to hours, in both juvenile and adult zebra finches[111,112]. Finally, in mice, levels of FOXP2 in the medial, but not the lateral, geniculate nucleus change after auditory stimulation with white noise, emphasizing that neural activity can regulate the expression of *Foxp2* in specific subsets of neurons in different species[115]. Together, these data support the notion that FOXP2 supports vocal behaviour by acting during the development of the underlying neural circuitry and in the same circuitry during adulthood.

To investigate possible causal relationships between *FOXP2* expression and vocal learning, FOXP2 levels were experimentally reduced using lentivirus-mediated RNA-interference in Area X of juvenile zebra finches throughout the sensorimotor song learning phase[20]. The *FOXP2* knockdown birds copied tutor songs only partially, imitating some song elements but omitting others. Moreover, the song elements that were imitated from tutor songs were less accurately copied than those copied by control birds, and song element production was more variable from rendition to rendition[20]. This variability of song production in zebra finches as a result of FOXP2 knockdown during development strikingly resembles the incomplete and inaccurate renditions of words and highly variable pronunciation[116] that is typical of DVD patients. Of note, it seems unlikely that knock down in Area X impairs the production of particular sounds, because song elements with similar acoustic features could be both badly and well imitated by the same finch[20]. FOXP2 levels were not manipulated during embryonic development in these experiments, but only when song control brain circuits were already largely assembled, suggesting that a reduction of FOXP2 affects postnatal function independently from effects on embryonic nervous system development.

Interestingly, mice with absent or reduced functional FOXP2 can also still produce the entire repertoire of ultrasonic distress and isolation calls, but at reduced intensities or rates[117]. The fact that the acoustic patterns of innate distress calls in mouse pups are not affected by FOXP2 levels underlines that FOXP2 does not primarily have a 'motor' function but instead, seems to be necessary for auditory–vocal motor integration, an essential prerequisite for vocal learning.

Role of FOXP2 in cortico–basal ganglia circuits. In Area X of the songbird brain, *FOXP2* is expressed in spiny neurons that exhibit many features of mammalian striatal medium spiny neurons. Spiny neurons in Area X are innervated by glutamatergic HVC neurons[118], which fire sparsely during singing, similar to the 'mirror neurons' identified in swamp sparrows[119] (*Melospiza georgiana*) (Supplementary information S6 (box)). The HVC–Area X projections onto spiny neurons are modulated presynaptically by midbrain dopaminergic input[110]. Because nigral dopamine acts on many behavioural systems, including reward learning, the integration of pallial glutamatergic and dopaminergic signals in *FOXP2*-expressing spiny neurons may be essential for fine-tuning song motor output to match the tutor song model. Modulation of *FOXP2* expression might result in upregulation or downregulation of neural plasticity-relevant genes that could in turn affect motor learning and motor performance through structural and functional changes of the spiny neurons. This hypothesis is supported by recent data showing that spiny neurons in adult Area X exhibit significantly fewer spines after receiving lentivirally-mediated *FOXP2* knock down than after control knock downs[120]. To investigate whether FOXP2 might also have a role in neural fate specification during neurogenesis, the lentivirus was injected into the ventricular zone, where striatal spiny neurons are born before migrating to Area X and the surrounding striatum. In spite of *FOXP2* knock down, neurons developed into spiny neurons that migrated and integrated into Area X, albeit carrying fewer spines than control neurons. These findings show that a reduction of FOXP2 levels in newborn neurons does not prevent them from differentiating, but influences synaptic spine density and, therefore, synaptic plasticity. Consistent with this interpretation, mice with experimentally reduced amounts of FOXP2 have altered synaptic plasticity in the striatum and show impaired motor learning[121].

These studies illustrate how animal models can be used to tease apart the organizational level of language at which a particular gene is required. In the case of *FOXP2* the aetiological mutations cause a disorder involving imperfect execution of orofacial gestures that produce speech sounds[105]. This could in principle be due to improper cranial motor neuron function. However, the functional studies in zebra finches instead point towards a role in postnatal cortico–basal ganglia circuits, which provide an entry point into unravelling the cellular and molecular mechanisms that are involved in the execution of orofacial gestures that produce speech sounds.

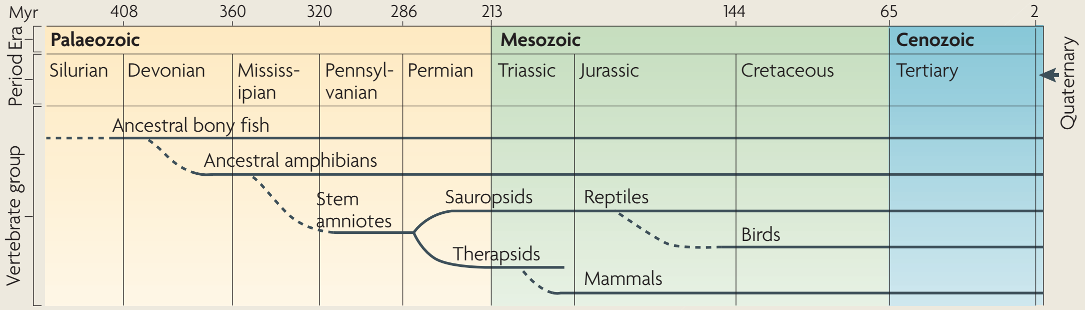
No single gene can be responsible for our ability to use a human-specific linguistic toolkit to communicate with each other (BOX 4). Investigating the role of genes operating at the different levels of organ systems and neural circuits required for language will bring us closer towards understanding how vocal communication works.

FOXP2 constitutes an example of a gene that is found to be relevant for human language and that can be studied in the songbird model system. Other human mutations associated with cognitive deficits are starting to be studied in songbirds[122]. Conversely, genes that have been identified in songbirds and that are relevant for singing[123] may be relevant for human cognitive function, including language, as is the case for the gene encoding a Rho guanine nucleotide exchange factor — expression of which in zebra finch Area X is regulated by singing[124], and mutations in which have been associated with mental retardation in humans[125]. The recent completion of the sequencing of the zebra finch genome[126,127] and associated studies will greatly enhance the power of such comparative approaches, as will the discovery of other genes related to language deficits, for example, stuttering[128]. The implications of the research into FOXP2 for the molecular evolution of birdsong and language are discussed in BOX 5.

Conclusions and future directions

Taken together, the research conducted in the decade since the review by Doupe and Kuhl[5] suggests that analogous mechanisms underlie auditory–vocal learning in humans and birds at the behavioural, neural, genetic and cognitive levels. These analogies are important for a number of reasons. First, they can provide insight into the evolution of brain and cognition (BOX 3). Further comparative neuroanatomical research is needed to establish the

Box 5 | **Molecular evolution of language and birdsong**



Comparative genetic studies can address how the ‘extra ingredients’ necessary for human language have been implemented biologically. The last common ancestor of humans and birds lived about 300 million years ago (see the figure). The similarity of basal ganglia circuits and their functions in amniotes is consistent with the idea that vocal learning in the divergent lineages of synapsids (leading to mammals) and diapsids (leading to birds) may have exapted existing pallial-basal ganglia features, including FOXP2’s role in the striatum. Comparing genes relevant for speech and learned birdsong may uncover shared key molecular networks that are relevant for vocal learning in distantly related species. Alternatively, one can compare genes and their functions between non-human and human primates, in order to find human-specific genes, including those relevant to speech and language. Of the approximately 23,000 human genes, the 50–100 that are unique to man[141] are unlikely to be solely responsible for the difference between human and non-human primates. This is why attention has turned towards orthologous genes that show signs of positive selection in the human lineage, including *FOXP2* (REF. 142).

Geschwind and colleagues[143] showed that in human cell lines, target genes are differentially regulated by the human FOXP2 version than by the chimpanzee FOXP2, and that chimpanzee brains express some of those target genes at different levels than human brains[143]. These constitute but a small subset of several hundred potential FOXP2 target genes that were discovered through target screening approaches employing neuronal-like cell lines and human embryonic tissues[144,145]. Thus, quantitative as well as qualitative changes in the molecular cascade controlled by transcription factors such as FOXP2 could be a source (but also a consequence) of evolutionary changes leading from the common ancestor to chimpanzee in one lineage and to humans in another. However, comparison of *FOXP2* sequences in vocal learning and non-vocal learning bird species did not reveal *FOXP2* sequence variants that segregated with the ability to imitate communication sounds[11]. This emphasizes the fact that although FOXP2 plays a role in song production, particular FOXP2 versions do not correlate with vocal learning in birds. Figure reproduced, with permission, from REF. 15 © 2005 Macmillan Publishers Ltd. All rights reserved. Myr, million years ago.

homologies between the avian and mammalian brains. In addition, comparative analyses of auditory–vocal learning and ‘syntax’ (BOX 2; Supplementary information S3 (box), S4 (box) and S5 (box)) are needed to reveal the evolutionary convergent mechanisms that are subserved by these homologous neural structures. Second, birdsong as an animal model for human speech opens up new ways to study the underlying neural and genetic mechanisms, because the songbird brain is accessible to invasive research techniques that, for obvious ethical reasons, are not available in human research. Third, the strong similarities between birdsong and speech are of great mutual heuristic value. For instance, human syntax begs the question as to whether there is a comparable structure (‘phonetical syntax’; Supplementary information S3 (box)) in birdsong. Another example is the discovery of a neural circuit specifically involved in subsong[38] (Supplementary information S2 (box)). Is there a similar neural specialization for babbling in human infants?

Neurobiological analyses of birdsong need to focus on the roles of the caudal pallium and the song system in auditory–vocal learning and production. Gene expression studies have advanced our knowledge of the avian brain, because they measure neuronal activation in awake animals and can provide an overall picture of brain activity. However, within-subject comparisons are limited with this method. At the moment, fMRI analyses of the avian brain, although allowing within-subject comparisons, lack resolution. We suggest that, in addition to single-unit recordings, multi-channel electrophysiological methods[129] are required to provide online analyses of neuronal activity in large numbers of neurons in large sections of the brain. Future research needs to focus on the role of sleep (Supplementary information S7 (box)) in both song learning in birds and in the acquisition of human speech and language. Electrophysiological analysis of both the song system and the caudal pallium during wakefulness and different stages of sleep in juvenile songbirds will be important. Also, the effects of sleep deprivation in song learning and language acquisition needs to be investigated. In addition, the possible role of mirror neuron systems (Supplementary information S6 (box)) in auditory–vocal learning in both humans and songbirds needs to be studied.

During the last few years, songbird research has fully entered the age of molecular genetics. The first songbird genome, that of the zebra finch, has been sequenced[127], and transgenesis is feasible, if inefficient[130]. The next decade will harness techniques such as RNA interference, microarrays and chromatin immunoprecipitation to gain insight into the molecular underpinnings of song learning and song production, identifying gene networks

Amniotes
The collective name for mammals, reptiles and birds that are characterized by four limbs, a spinal column and embryos that develop within a fluid-filled cavity that is enclosed by membranes (‘amnion’).

Transgenesis
The introduction of an exogenous gene — a transgene — into an organism which results in expression of the new gene and its transmission into the next generation.

Non-vocal learner
A bird species that does not learn its vocalizations.

Recursion
A term used by linguists to refer to the embedding of a structure into the same type of structure — for example, embedding a sentence into another sentence.

Phonological
In a narrow sense, referring to the set of physical and psychological features of a unit of speech. In a broader sense, referring to the acoustic characteristics of a unit of sound.

associated with developing vocal learning circuits and their functions, manipulating them and comparing them in different species. Molecular studies in birds comparing non-vocal learners with vocal learners are promising particularly exciting insights into the evolution of vocal learning and perhaps also into other analogies between humans and songbirds.

Another important line of future research concerns the analogies (if any) between linguistic structures and the syntax of avian vocalizations, for example, recursion[3,131–133] (Supplementary information S5 (box)). European starlings (*Sturnus vulgaris*), a songbird species, were successfully trained to discriminate between artificial song sequences designed to reflect recursive rules and sequences that reflected non-recursive rules[131]. However, a study in zebra finches suggested that birds were not responding to the recursion, but to the phonological pattern[133]. A recent demonstration of cultural evolution in birdsong[29] revived the idea of 'innate grammar', but the results actually point towards how perceptual and motor constraints without assuming innate grammar, could shape species-specific songs when going through a few generations. Taken together, comparative neural, genetic and linguistic studies should lead to a productive research program concerning the biology of birdsong, speech and language.

1. Darwin, C. *The Descent of Man and Selection in Relation to Sex.* (Murray, London, 1882).
2. Bolhuis, J. J. & Wynne, C. D. L. Can evolution explain how minds work? *Nature* **458**, 832–833 (2009).
3. Hauser, M. D., Chomsky, N. & Fitch, W. T. The faculty of language: what is it, who has it, and how did it evolve? *Science*, **298**, 1569–1579 (2002).
A thought-provoking opinion article on the possible evolution of language, with suggested criteria for language, including recursion.
4. Fitch, W. T. The evolution of speech: a comparative review. *Trends Cogn. Sci.* **4**, 258–267 (2000).
5. Doupe, A. J. & Kuhl, P. K. Birdsong and human speech: common themes and mechanisms. *Annu. Rev. Neurosci.* **22**, 567–631 (1999).
The first detailed review of the many behavioural and neural parallels between birdsong and human speech.
6. Brainard, M. S. & Doupe, A. J. What songbirds teach us about learning. *Nature* **417**, 351–358 (2002).
7. Bolhuis, J. J. & Gahr, M. Neural mechanisms of birdsong memory. *Nature Rev. Neurosci.* **7**, 347–357 (2006).
8. Yip, M. The search for phonology in other species. *Trends Cogn. Sci.* **10**, 442–446 (2006).
9. Balter, M. Animal communication helps reveal the roots of language. *Science* **328**, 969–971 (2010).
10. Wilbrecht, L. & Nottebohm, F. Vocal learning in birds and humans. *Ment. Retard. Dev. Disabil. Res. Rev.* **9**, 135–148 (2003).
11. Scharff, C. & Haesler, S. An evolutionary perspective on FoxP2: strictly for the birds? *Curr. Opin. Neurobiol.* **15**, 694–703 (2005).
12. Okanoya, K. Song syntax in Bengalese finches: proximate and ultimate analyses. *Adv. Study Behav.* **34**, 297–346 (2004).
13. Okanoya, K. Language evolution and an emergent property. *Curr. Opin. Neurobiol.* **17**, 271–276 (2007).
14. Reiner, A. *et al.* Revised nomenclature for avian telencephalon and some related brainstem nuclei. *J. Comp. Neurol.* **473**, 377–414 (2004).
A landmark paper presenting a complete overhaul of the nomenclature of the avian brain, indicating possible homologies with the brain of mammals, including humans.
15. Jarvis, E. D. *et al.* Avian brains and a new understanding of vertebrate brain evolution. *Nature Rev. Neurosci.* **6**, 151–159 (2005).
An important review of the consequences of the new nomenclature of the avian brain for the evolution of brain and behaviour, and our view of the 'birdbrain'.
16. Mooney, R. Neural mechanisms for learned birdsong. *Learn. Mem.* **16**, 655–669 (2009).
An excellent contemporary review that synthesises recent findings to present a state-of-the-art view of the neural mechanisms of song learning.
17. Doupe, A. J., Perkel, D. J., Reiner, A. & Stern, E. A. Birdbrains could teach basal ganglia research a new song. *Trends Neurosci.* **28**, 353–363 (2005).
18. Lai, C. S. L., Fisher, S. E., Hurst, J. A., Vargha-Khadem, F. & Monaco, A. P. A forkhead-domain gene is mutated in a severe speech and language disorder. *Nature* **413**, 519–523 (2001).
The first demonstration of a link between a specific gene, *FOXP2*, and a human speech disorder called developmental verbal dyspraxia.
19. Fisher S. E. & Scharff, C. FOXP2 as a molecular window into speech and language. *Trends Genet.* **25**, 166–177 (2009).
20. Haesler, S. *et al.* Incomplete and inaccurate vocal imitation after knockdown of FoxP2 in songbird basal ganglia nucleus Area X. *PLoS Biol.* **5**, e321 (2007).
The first *in vivo* gene-function analysis in songbirds, demonstrating that lentivirally-mediated knock down of the *FOXP2* gene impairs the complete and accurate imitation of tutor song during song learning.
21. Fernald, R. D. Casting a genetic light on the evolution of eyes. *Science* **313**, 1914–1918 (2006).
22. Pearson, K. G. Common principles of motor control in vertebrates and invertebrates. *Annu. Rev. Neurosci.* **16**, 265–297 (1993).
23. Marler, P. in *The Epigenesis of Mind: Essays on Biology and Cognition* (eds Carey, S. & Gelman, R.) 37–66 (Lawrence Erlbaum Associates, Hillsdale, New Jersey, 1991).
24. Marler, P. & Peters, S. S. in *The Comparative Psychology of Audition: Perceiving Complex Sounds* (eds Hulse, S. & Dooling, R.) 243–273 (Lawrence Erlbaum, Hillsdale, New Jersey, 1989).
25. Pinker, S. *The Language Instinct: How the Mind Creates Language* (W. Morrow and Co., New York, 1994).
26. Goller, F & Cooper B. G. In *Neuroscience of Birdsong* (eds Zeigler, H. P. & Marler, P.) 99–114 (Cambridge Univ. Press, New York, 2008).
27. Konishi, M. The role of auditory feedback in the control of vocalization in the white-crowned sparrow. *Z. Tierpsychol.* **22**, 770–783 (1965).
28. Catchpole, C. K. & Slater, P. J. B. *Bird Song: Biological Themes and Variations* 2nd edn (Cambridge Univ. Press, Cambridge, 2008).
29. Feher, O., Wang, H., Saar, S., Mitra, P. P. & Tchernichovski, O. *De novo* establishment of wild-type song culture in the zebra finch. *Nature* **459**, 564–568 (2009).
A demonstration that species-specific songs can emerge through a few generations of individual learning in the absence of correct external models.
30. Hurford, J. R. The Evolution of the critical period for language acquisition. *Cognition* **40**, 159–201 (1991).
31. Kipper, S. & Kiefer, S. Age-related changes in birds' singing styles: on fresh tunes and fading voices? *Adv. Study Behav.* **41**, 77–118 (2010).
32. Funabiki, Y. & Funabiki, K. Factors limiting song acquisition in adult zebra finches. *Dev. Neurobiol.* **69**, 752–759 (2009).
33. Marler, P. Three models of song learning: evidence from behaviour. *J. Neurobiol.* **33**, 501–516 (1997).
34. Hultsch, H. & Todt, D. in *Nature's Music — The Science of Birdsong* (eds Marler, P. & Slabbekoorn, H.) 80–107 (Academic Press, Amsterdam & Boston, 2004).
35. Roper, A. & Zann, R. The onset of song learning and song tutor selection in fledgling zebra finches. *Ethology* **112**, 458–470 (2006).
36. Liu, W. C. & Nottebohm, F. A learning program that ensures prompt and versatile vocal imitation. *Proc. Natl Acad. Sci. USA* **104**, 20398–20403 (2007).
37. Tchernichovski, O., Mitra, P. P., Lints, T. & Nottebohm, F. Dynamics of the vocal imitation process: how a zebra finch learns its song. *Science* **291**, 2564–2569 (2001).
38. Aronov, D., Andalman, A. S. & Fee, M. S. A specialized forebrain circuit for vocal babbling in the juvenile songbird. *Science* **320**, 630–634 (2008).
39. Deacon, T. W. Evolutionary perspectives on language and brain plasticity. *J. Commun. Disord.* **33**, 273–291 (2000).
40. Hage, R. S. Neural networks involved in the generation of vocalization. *Handb. Behav. Neurosci.* **19**, 339–349 (2009).
41. Goldstein, M. H., King, A. P. & West, M. J. Social interaction shapes babbling: testing parallels between birdsong and speech. *Proc. Natl Acad. Sci. USA* **100**, 8030–8035 (2003).
42. Kuhl, P. K. & Rivera-Gaxiola, M. Neural substrates of early language acquisition. *Annu. Rev. Neurosci.* **31**, 511–534 (2008).
43. Smith, V. A., King, A. P. & West, M. J. A role of her own: female cowbirds, Molothrus ater, influence the development and outcome of song learning. *Anim. Behav.* **60**, 599–609 (2000).
44. Levelt, W. L. M. in *The Neurocognition of Language*. (eds Brown, C. M. & Hagoort, P.) 83–122 (Oxford Univ. Press, Oxford, 1999).
45. Fitch, W. T., Hauser, M. D. & Chomsky, N. The evolution of the language faculty: clarifications and implications. *Cognition* **97**, 179–210 (2005).
46. Pinker, S. & Jackendoff, R. The faculty of language: what's special about it? *Cognition* **95**, 201–236 (2005).
47. Staal, F. *Rules Without Meaning. Ritual, Mantras and the Human Sciences* (Peter Lang, New York, 1989).
48. Kumar, S. & Hedges, S. B. A molecular timescale for vertebrate evolution. *Nature* **392**, 917–920 (1998).
49. Brainard, M. S. & Doupe, A. J. Auditory feedback in learning and maintenance of vocal behaviour. *Nature Rev. Neurosci.* **1**, 31–40 (2000).
An important review of the evidence pertaining to the role of auditory feedback in birdsong learning and production.
50. Chew, S. J., Vicario, D. S. & Nottebohm, F. A large-capacity memory system that recognizes the calls and songs of individual birds. *Proc. Natl Acad. Sci. USA* **93**, 1950–1955 (1996).
51. Bolhuis, J. J., Zijlstra, G. G. O., Den Boer-Visser, A. M. & Van der Zee, E. A. Localized neuronal activation in the zebra finch brain is related to the strength of song learning, *Proc. Natl Acad. Sci. USA* **97**, 2282–2285 (2000).
52. Bolhuis, J. J., Hetebrij, E., Den Boer-Visser, A. M., De Groot, J. H. & Zijlstra, G. G. O. Localized immediate early gene expression related to the strength of song learning in socially reared zebra finches, *Eur. J. Neurosci.* **13**, 2165–2170 (2001).
53. Terpstra, N. J., Bolhuis, J. J. & den Boer-Visser, A. M. An analysis of the neural representation of bird song memory. *J. Neurosci.* **24**, 4971–4977 (2004).
54. Phan, M. L., Pytte, C. L. & Vicario, D. S. Early auditory experience generates long-lasting memories that may subserve vocal learning in songbirds. *Proc. Natl Acad. Sci. USA* **103**, 1088–1093 (2006).
55. Demonet, J. F., Thierry, G. & Cardebat, D. Renewal of the neurophysiology of language: functional neuroimaging. *Physiol. Rev.* **85**, 49–95 (2005).
56. Viceic, D. *et al.* Human auditory belt areas specialized in sound recognition: a functional magnetic resonance imaging study. *Neuroreport* **17**, 1659–1662 (2006).

57. Karten, H. J. Evolutionary developmental biology meets the brain: the origins of mammalian cortex. *Proc. Natl Acad. Sci. USA* **94**, 2800–2804 (1997).
58. Reiner, A., Yamamoto, K. & Karten, H. J. Organization and evolution of the avian forebrain. *Anat. Rec. A Discov. Mol. Cell. Evol. Biol.* **287**, 1080–1102 (2005).
59. Jarvis, E. D. Learned birdsong and the neurobiology of human language. *Ann. NY Acad. Sci.*, **1016**, 749–777 (2004).
60. Okanoya, K. & Merker, B. in *Emergence of Communication and Language* (eds Lyon, C., Nehaniv, C. L. & Cangelosi, A.) 421–434 (Springer Verlag, London, 2007).
61. Dehaene-Lambertz, G. *et al.* Functional organization of perisylvian activation during presentation of sentences in preverbal infants. *Proc. Natl Acad. Sci. USA* **103**, 14240–14245 (2006).
62. Gobes, S. M. H. & Bolhuis, J. J. Bird song memory: a neural dissociation between song recognition and production. *Curr. Biol.* **17**, 789–793 (2007).
63. Volman, S. F. Development of neural selectivity for birdsong during vocal learning. *J. Neurosci.* **13**, 4737– 4747 (1993).
64. Nick, T. A. & Konishi, M. Neural song preference during vocal learning in the zebra finch depends on age and state. *J. Neurobiol.* **62**, 231–242 (2005).
65. Gentner, T. Q., Hulse, S. H., Bentley, G. E. & Ball, G. Individual vocal recognition and the effect of partial lesions to HVc on discrimination, learning, and categorization of conspecific song in adult songbirds. *J. Neurobiol.* **42**, 117–133 (2000).
66. Nottebohm, F., Stokes, T. & Leonard, C. M. Central control of song in the canary. *J. Comp. Neurol.* **165**, 457–486 (1976).
67. Gobes, S.M.H., Zandbergen, M.A. & Bolhuis, J.J. Memory in the making: Localized brain activation related to song learning in young songbirds. *Proc. Roy. Soc. Lond., B.* **277**, 3343-3351 (2010).
68. Nottebohm, F. A brain for all seasons: cyclical anatomical changes in song control nuclei of the canary brain. *Science* **214**, 1368–1370 (1981).
69. Solis, M. M., Brainard, M. S., Hessler, N. A. & Doupe, A. J. Song selectivity and sensorimotor signals in vocal learning and production. *Proc. Natl Acad. Sci. USA,* **97**, 11836–11842 (2000).
70. Margoliash, D. & Konishi, M. Auditory representation of autogenous song in the song system of white-crowned sparrows. *Proc. Natl Acad. Sci. USA* **82**, 5997–6000 (1985).
71. Margoliash, D. Preference for autogenous song by auditory neurons in a song system nucleus of the white-crowned sparrow. *J. Neurosci.* **6**, 1643–1661 (1986).
72. Scharff, C., Nottebohm, F. & Cynx, J. Conspecific and heterospecific song discrimination in male zebra finches with lesions in the anterior forebrain pathway. *J. Neurobiol.* **36**, 81–90 (1998).
73. Gobes, S. M. H., Bolhuis, J. J., Terpstra, N. J., den Boer-Visser, A. M. & Zandbergen, M. A. Immediate early gene expression in the zebra finch song system in response to familiar and novel song. *Soc. Neurosci. Abstr*. **33**, 646.13 (2007).
74. Imada, T. *et al.* Infant speech perception activates Broca's area: a developmental magnetoencephalography study. *Neuroreport* **17**, 957–962 (2006).
75. Brainard, M. S. & Doupe, A. J. Interruption of a basal ganglia–forebrain circuit prevents plasticity of learned vocalizations. *Nature* **404**, 762–766 (2000).
76. Möttönen, R. & Watkins K. E. Motor representations of articulators contribute to categorical perception of speech sounds. *J. Neurosci.* **29**, 9819 -9825 (2009).
77. Bauer, E. E., Coleman, M. J., Roberts, T. F., Roy, A., Prather, J. F. & Mooney, R. A synaptic basis for auditory-vocal integration in the songbird. *J. Neurosci.* **28**, 1509–1522 (2008).
78. Coleman, M. J. & Mooney, R. Synaptic transformations underlying highly selective auditory representations of learned birdsong. *J. Neurosci.* **24**, 7251–7265 (2004).
79. Coleman, M. J., Roy, A., Wild, J. M. & Mooney, R. Thalamic gating of auditory responses in telencephalic song control nuclei. *J. Neurosci.* **27**, 10024–10036 (2007).
80. Fortune, E. S. & Margoliash, D. Parallel pathways and convergence onto HVc and adjacent neostriatum of adult zebra finches (*Taeniopygia guttata*). *J. Comp. Neurol.* **360**, 413–441 (1995).
81. Williams, H. & Nottebohm, F. Auditory response in avian vocal motor neurons: a motor theory for song perception in birds. *Science* **229**, 279–282 (1985).
82. Fadiga, L. Speech listening specifically modulates the excitability of tongue muscles: a TMS study. *Eur. J. Neurosci.* **15**, 399–402 (2002).
83. Scharff, C. & Nottebohm, F. A comparative study of the behavioral deficits following lesions of various parts of the zebra finch song system: implications for vocal learning. *J. Neurosci.* **11**, 2896–2913 (1991).
84. Bottjer, S. W., Miesner, E. A. & Arnold, A. P. Forebrain lesions disrupt development but not maintenance of song in passerine birds. *Science* **224**, 901–903 (1984).
85. Sohrabji, F, Nordeen E. J. & Nordeen, K. W. Selective impairment of song learning following lesions of a forebrain nucleus in the juvenile zebra finch. *Behav. Neural. Biol.* **53**, 51–63 (1990).
86. Troyer, T. W. & Bottjer, S. W. Birdsong: models and mechanisms. *Curr. Opin. Neurobiol.* **11**, 721–726 (2001).
87. Dave, A. S. & Margoliash, D. Song replay during sleep and computational rules for sensorimotor vocal learning. *Science* **290**, 812–816 (2000).
This study demonstrates 'replay' of singing-induced neuronal activity during sleep in zebra finches.
88. Hessler, N. A. & Doupe, A. J. Singing-related neural activity in a dorsal forebrain-basal ganglia circuit of adult zebra finches. *J. Neurosci.* **19**, 10461–10481 (1999).
89. Katz, L. C. & Gurney, M. E. Auditory responses in the zebra finch's motor system for song. *Brain Res.* **221**, 192–197 (1981).
90. McCasland, J. S. & Konishi, M. Interaction between auditory and motor activities in an avian song control nucleus. *Proc. Natl Acad. Sci. USA* **78**, 7815–7819 (1981).
91. Doupe, A. J. & Konishi, M. Song-selective auditory circuits in the vocal control system of the zebra finch. *Proc. Natl Acad. Sci. USA* **88**, 11339–11343 (1991).
92. Leonardo, A. Experimental test of the birdsong error-correction model. *Proc. Natl Acad. Sci. USA* **101**, 16935–16940 (2004).
The author used a combination of behavioural and electrophysiological techniques to show that the AFP does not provide the feedback error itself. After this study, efforts were directed towards detecting instructive signals in the AFP.
93. Gale, S. D. & Perkel, D. J. A basal ganglia pathway drives selective auditory responses in songbird dopaminergic neurons via disinhibition. *J. Neurosci.* **30**, 1027–1037 (2010).
94. Keller, G. B. & Hahnloser, R. H. R. Neural processing of auditory feedback during vocal practice in a songbird. *Nature* **457**, 187–190 (2009).
This study showed that there are neurons in auditory regions of the songbird brain that are sensitive to changes in auditory feedback during song learning.
95. Williams, H. & Mehta, N. Changes in adult zebra finch song require a forebrain nucleus that is not necessary for song production. *J. Neurobiol.* **39**, 14–28 (1999).
96. Sober, S. J. & Brainard, M. S. Adult birdsong is actively maintained by error correction. *Nature Neurosci.* **12**, 927–931 (2009).
97. Doya, K. & Sejnowski, T. J. A novel reinforcement model of birdsong vocalization learning. *Adv. Neural Inf. Process. Syst.* **7**, 101–108 (1995).
98. Tumer, E. C. & Brainard, M. S. Performance variability enables adaptive plasticity of 'crystallized' adult birdsong. *Nature* **450**, 1240–1244 (2007).
99. Andalman, A. S. & Fee, M. S. A basal ganglia-forebrain circuit in the songbird biases motor output to avoid vocal errors. *Proc. Natl Acad. Sci. USA* **106**, 12518–12523 (2009).
Using pharmacological manipulation, this study demonstrated that the song system nucleus LMAN provides instructive signals that can be used to correct song if it does not match the template.
100. Christoffels, I. K., Formisano, E. & Schiller, N. O. Neural correlates of verbal feedback processing: an fMRI study employing overt speech. *Hum. Brain Mapp.* **28**, 868–879 (2007).
101. Magno, E., Foxe, J. J., Molholm, S., Robertson, I. H. & Garavan, H. The anterior cingulate and error avoidance. *J. Neurosci.* **26**, 4769 – 4773 (2006).
102. Chater, N., Reali, F. & Christiansen. M. H. Restrictions on biological adaptation in language evolution. *Proc. Natl Acad. Sci. USA* **106**, 1015–1020 (2009).
103. Vernes, S. C. & Fisher, S. E. Unravelling neurogenetic networks implicated in developmental language disorders. *Biochem. Soc. Trans.* **37**, 1263–1269 (2009).
104. Vernes, S. C. *et al.* A functional genetic link between distinct developmental language disorders. *N. Engl. J. Med.* **359**, 2337–2345 (2008).
105. Vargha-Khadem, F., Gadian, D. G., Copp, A. & Mishkin, M. FOXP2 and the neuroanatomy of speech and language. *Nature Rev. Neurosci.* **6**, 131–138 (2005).
106. White, S. A., Fisher, S. E., Geschwind, D. H., Scharff, C. & Holy, T. E. Singing mice, songbirds, and more: models for FOXP2 function and dysfunction in human speech and language. *J. Neurosci.* **26**, 10376–10379 (2006).
107. Hannenhalli, S. & Kaestner, K. H. The evolution of Fox genes and their role in development and disease. *Nature Rev. Genet.* **10**, 233–240 (2009).
108. Rochefort, C., He, X., Scotto-Lomassese, S. & Scharff, C. Recruitment of FoxP2-expressing neurons to area X varies during song development. *Dev. Neurobiol.* **67**, 809–817 (2007).
109. Kotz, S. A. & Schwartze, M. Cortical speech processing unplugged: a timely subcortico-cortical framework. *Trends Cogn. Sci.* **14**, 392–399 (2010).
110. Person, A. L., Gale, S. D., Farries, M. A. & Perkel, D. J. Organization of the songbird basal ganglia, including area X. *J. Comp. Neurol.* **508**, 840–866 (2008).
111. Teramitsu, I. & White, S. A. FoxP2 regulation during undirected singing in adult songbirds. *J. Neurosci.* **26**, 7390–7394 (2006).
The first report that FoxP2 expression is modulated in adult zebra finches by singing, demonstrating a regulatory role of FoxP2 in adult brain circuitry.
112. Teramitsu, I., Poopatanapong, A., Torrisi, S. & White, S. A. Striatal FoxP2 is actively regulated during songbird sensorimotor learning. *PLoS ONE* **5**, e8548 (2010).
113. Haesler, S. *et al. FoxP2* expression in avian vocal learners and non-learners. *J. Neurosci.* **24**, 3164 –3175 (2004).
114. Iyengar, S., Viswanathan, S. S. & Bottjer, S. Development of topography within song control circuitry of zebra finches during the sensitive period of song learning. *J. Neurosci.* **19**, 6037–6057 (1999).
115. Horng, S. *et al.* Differential gene expression in the developing lateral geniculate nucleus and medial geniculate nucleus reveals novel roles for Zic4 and Foxp2 in visual and auditory pathway development. *J. Neurosci.* 29 13672–13683 (2009).
116. Marquardt, T. P., Jacks, A. & Davis, B. L. Token-to-token variability in developmental apraxia of speech: three longitudinal case studies. *Clin. Linguist. Phon*. **18**, 127–144 (2004).
117. Gaub, S., Groszer, M. Fisher, S. E. & Ehret, G. The structure of innate vocalizations in Foxp2 deficient mouse pups. *Genes Brain Behav.* **9**, 390–401 (2010).
118. Farries, M. A. Ding, L. & Perkel, D. J. Evidence for "direct" and "indirect" pathways through the song system basal ganglia. *J. Comp. Neurol.* **484**, 93–104 (2005).
119. Prather, J.F, Peters, S., Nowicki, S. & Mooney, R. Precise auditory-vocal mirroring in neurons for learned vocal comunication. *Nature* **451**, 305–310 (2008).
The first demonstration of auditory–vocal mirror neurons in birds with detailed neuroanatomical and electrophysiological analyses.
120. Schulz, S. B., Haesler, S., Scharff, C. & Rochefort, C. Knockdown of FoxP2 alters spine density in Area X of the zebra finch. *Genes Brain Behav.* 6 Jul 2010 (doi: 10.1111/j.1601-183X.2010.00607.x).
121. Groszer, M. *et al.* Impaired synaptic plasticity and motor learning in mice with a point mutation implicated in human speech deficits. *Curr. Biol.* **18**, 354–362 (2008).
122. Winograd, C., Clayton, D. & Ceman, S. Expression of fragile X mental retardation protein within the vocal control system of developing and adult male zebra finches. *Neuroscience* **157**, 132–142 (2008).
123. White, S. A. Genes and vocal learning. *Brain Lang*. 12 Nov 2009 (doi:10.1016/j.bandl.2009.10.002).
124. Wada, K. *et al.* A molecular neuroethological approach for identifying and characterizing a cascade of behaviorally regulated genes. *Proc. Natl Acad. Sci. USA,* **103**, 15212–15217 (2006).
125. Kalscheuer, V. M. *et al.* A balanced chromosomal translocation disrupting ARHGEF9 is associated with epilepsy, anxiety, aggression, and mental retardation. *Hum. Mutat.* **30**, 61–68 (2009).
126. Lovell P. V., Clayton D. F., Replogle K.L & Mello C. V. Birdsong "transcriptomics": neurochemical specializations of the oscine song system. *PLoS ONE* **3**, e3440 (2008).
127. Warren, W. C. *et al.* The genome of a songbird. *Nature* **464**, 757–762 (2010).

128. Kang C. *et al.* Mutations in the lysosomal enzyme-targeting pathway and persistent stuttering. *N. Engl. J. Med.* **362**, 677–685 (2010).
129. Beckers, G. J. L. & Gahr, M. Neural processing of short-term recurrence in songbird vocal communication. *PLoS ONE* **5**, e11129 (2010).
130. Agate R. J., Scott B. B., Haripal B., Lois C. & Nottebohm F. Transgenic songbirds offer an opportunity to develop a genetic model for vocal learning. *Proc. Natl Acad. Sci. USA* **106**, 17963–17967 (2009).
131. Gentner, T., Fenn., K., Margoliash, D. & Nusbaum, H. Recursive syntactic pattern learning by songbirds. *Nature* **440**, 1204–1207 (2005).
An intriguing study into the ability of starlings to recognize recursive patterns in conspecific vocalizations. See also references 132 and 133.
132. Corballis, M. C. Recursion, language, and starlings. *Cogn. Sci.* **31**, 697–704 (2007).
133. van Heijningen, C. A. A., de Visser, J., Zuidema, W. & ten Cate, C. Simple rules can explain discrimination of putative recursive syntactic structures by a songbird species. *Proc. Natl Acad. Sci. USA* **106**, 20538–20543 (2009).
134. Tomasello, M. *Constructing A Language: A Usage-Based Theory of Language Acquisition.* (Harvard Univ. Press, Cambridge, Massachusetts, 2003).
135. Kao. M. H. & Brainard, M.S. Lesions of an avian basal ganglia circuit prevent context-dependent changes to song variability. *J. Neurophysiol.* **96**, 1441–1455 (2006).
136. Kao M. H., Wright B. D. & Doupe A. J. Neurons in a forebrain nucleus required for vocal plasticity rapidly switch between precise firing and variable bursting depending on social context. *J. Neurosci.* **28**, 13232–13247 (2008).
137. Hahnloser, R. H. R., Kozhevnikov, A. & Fee, M. S. An ultra-sparse code underlies the generation of neural sequences in a songbird. *Nature* **419**, 65–70 (2002).
138. Gibb, L., Gentner, T. Q. & Abarbanel, H. D. I. Inhibition and recurrent excitation in a computational model of sparse bursting in song nucleus HVC. *J. Neurophysiol.* **102**, 1748–1762 (2009).
139. Lewicki, M. S. & Arthur, B. J. Hierarchical organization of auditory temporal context sensitivity. *J. Neurosci.* **16**, 6987–6998 (1996).
140. Nishikawa, J., Okada, M. & Okanoya, K. Population coding of song element sequence in the Bengalese finch HVC. *Eur. J. Neurosci.* **27**, 3273–3283 (2008).
141. Stahl, P. D. & Wainszelbaum, M. J. Human-specific genes may offer a unique window into human cell signaling *Sci. Signal.* **2**, pe59 (2009).
142. Enard W. *et al.* Molecular evolution of FOXP2, a gene involved in speech and language. *Nature* **418**, 869–872 (2002).
143. Konopka, G. *et al.* Human-specific transcriptional regulation of CNS development genes by FOXP2. *Nature* **462**, 213–217 (2009).
144. Spiteri E. *et al.* Identification of the transcriptional targets of FOXP2, a gene linked to speech and language, in developing human brain. *Am. J. Hum. Genet.* **81**, 1144–1157 (2007).
145. Vernes, S. C. *et al.* High-throughput analysis of promoter occupancy reveals direct neural targets of FOXP2, a gene mutated in speech and language disorders. *Am. J. Hum. Genet.* **81**, 1232–1250 (2007).

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FURTHER INFORMATION

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