The existence of culturally transmitted languages and dialects provides evidence that speech is learned, and that this learning must depend on hearing. Songbirds, like humans, show evidence in their songs of learned dialects. Even more compelling are experiments in which birds learn the songs of unrelated adults of the same species or, in some cases, of different species to which they are exposed during development. So, although speech and birdsong clearly evolved independently and differ in many ways, they share a strong dependence on auditory experience not found in the vocal behaviour of many other animals.

Hearing the voice of others as well as one’s own is required for vocal learning. In songbirds, these two components of learning can be quite separated in time. First, during an initial, ‘sensory’ phase of learning, birds listen to the sounds of the adult songs to which they are exposed, and form an internal representation of song—a ‘song template’. This memory of song can be derived from a single or multiple adult ‘tutors’, or even from taped renditions of song. Birds raised in the complete absence of tutor song produce abnormal and simplified ‘isolate’ songs. In humans, the vocalizations of children with normal hearing who are deafened without exposure to human speech are also highly abnormal. So birdsong, like speech, depends on experience of the vocalizations of other individuals.

During the second, ‘sensorimotor’ phase of song learning, birds begin to sing, and gradually refine their initially variable and noisy vocalizations using auditory feedback, until their song approximates the tutor song, with some improvisations of their own. Birds must be able to hear themselves for this vocal refinement; if they are deafened after exposure to tutor song but before vocal practice, they develop abnormal songs that show no evidence of learning. Human speech learning shows a similar requirement for auditory feedback. For instance, if children become deaf even late in childhood, speech deteriorates markedly. These findings provide evidence that, in humans as in songbirds, the sounds produced by the individuals themselves are essential for normal vocal development.
Language and speech compared with birdsong

We use 'speech' to refer specifically to those components of human language that are involved in the sensorimotor control of the vocal system, not with semantics; 'language' refers to complex strings of words, ordered by the rules of grammar, to convey meaning. Language is typically mediated by speech, although it does not depend on it; for example, American Sign Language and writing both enable rich semantic communication without vocalization. The most compelling and best-studied parallels have been found between birdsong and human speech. These parallels include the demonstration of both perceptual and vocal motor learning, the existence of critical periods and innate predispositions for learning, the influence of social factors, and the presence of complex and in some cases homologous neural substrates for learning. However, although song is used for communication (conveying information about breeding status, identity, territorial ownership and other ecologically important factors), there is little evidence that elements of song can be used in a combinatorial manner to convey the kind of rich and flexible semantic content that characterizes language. A possible exception comes from the study of parrots and other members of the order Psittaciformes, which (at least in a laboratory setting) can be trained to use a 'vocabulary' of learned vocalizations in an apparently meaningful manner.

Box 1 | Language and speech compared with birdsong

In summary, behavioural experiments in songbirds suggest that when learning to sing, birds first form an internalized song memory or template, and then shape their vocal motor output by comparing auditory feedback of their own vocalizations with this template (FIG. 2). Comparison of the extent of the mismatch between the developing song and the template results in an appropriate instructive signal, which drives adaptive changes in the song motor program until the vocal output matches the internal model of the song.

Stabilization of adult vocal behaviour

Once speech and birdsong are learned, they often remain remarkably stable. For example, it is notoriously difficult to alter the accent of speech or to develop fluency in a new language in adulthood. Likewise, in many songbird species, the detailed structure of learned song normally remains unchanging in adulthood, regardless of continuing exposure to different acoustic models. This raises the questions of what causes the stabilization of a behaviour so clearly subject to modification by experience during learning, and of whether the processes involved in song learning are retained in the adult brain.

In principle, the stabilization of song could reflect loss of plasticity in the parts of the brain responsible for vocal motor control, such that they become 'hard-wired' and impervious to the further influence of experience (FIG. 3a). Alternatively, adult vocalizations may remain stable not because of developmental loss of plasticity in vocal control centres, but rather because vocalizations are actively maintained in their learned state. According to this model, adult song continues to be evaluated by auditory feedback, and does not change because it is well matched to an unchanging perceptual song model or template (FIG. 3b). For humans, there is evidence for a tight link between perception and production. For instance, adults have trouble accurately perceiving and producing sounds that are not used systematically in their native language, and better perceptual discrimination is correlated with better pronunciation.

A wealth of evidence supports the idea of critical periods for tutor song memorization in songbirds and for perceptual learning of speech sounds in humans. So the problem in changing adult vocalizations may not be an incapacity to alter vocal production, but rather, in addition, an incapacity to create new perceptual templates to which vocalizations can be matched.

Plasticity of adult song

In adult zebra finches, removal of auditory feedback by deafening results in a gradual deterioration of song, in some cases to a point where it is no longer recognizable as the same song as before deafening. Likewise, for humans, speech gradually deteriorates following profound hearing loss in adulthood, in some cases to a point of unintelligibility. These data show that the motor circuitry underlying the production of adult song (and speech) is not 'hard-wired', and indicate instead a continued influence of auditory feedback on adult vocalizations.

There is naturally occurring variability in the influence of auditory feedback on adult song, for instance, white-crowned sparrows can maintain their song with no notable deterioration for up to one and a half years after deafening. In these birds, song may have become truly independent of experience, or might be maintained by alternative sources of sensory feedback, such as proprioceptive signals from the vocal tract. In contrast to the white-crowned sparrow song, the more complex and variable songs of adult Bengalese finches and canaries deteriorate even more rapidly than zebra finch songs after loss of hearing. Unlike 'critical-period learners' such as the zebra finch, canaries and other 'open-learners' can acquire new songs in adulthood. A high degree of adult sensitivity to loss of hearing may be a concomitant of such open-ended song learning.
deafening may cause changes in social status, stress levels or amounts of singing. These, in turn, might have hormonal or trophic consequences that could cause changes in neurogenesis or other disruptions of the circuit for vocal motor control. Another plausible source of ‘induced drift’ would be centrally propagating trophic consequences associated with deafening, which typically involves damaging or removing the cochlea. It is difficult to rule out such indirect effects, and indeed there is evidence that hearing status or amount of singing can affect testosterone levels, the expression of trophic factors, and the turnover of newly generated neurons in the song control nucleus HVc (abbreviation used as the proper name).18,36,37.

Do adults match vocal output to a template?

In principle, any combination of the processes outlined in the three models described above (Fig. 4a–c) could contribute to the vocal deterioration that follows deafening. A manipulation that is potentially valuable for differentiating between these possibilities is alteration, rather than elimination, of auditory feedback. Leonardo and Konishi showed that perturbation of auditory feedback causes a gradual deterioration of adult zebra

What is the nature of the influence of auditory feedback in adulthood? One plausible explanation for the deterioration of vocalizations that occurs following deafening is that various biological processes contribute to a gradual ‘passive drift’ in the central and/or peripheral components of the motor circuitry for vocal production. These processes could include any alterations of neuronal structure or synaptic properties that would influence the functional connectivity of the vocal motor circuitry. For example, in songbirds, one potential source of central neural drift is the well documented incorporation of new neurons in the adult avian brain. Normally, evaluation of auditory feedback would be used to correct for such sources of drift, and to keep the song motor program calibrated. However, in deafened birds this corrective signal is not available and a gradual accumulation of changes in the motor circuit would lead to a progressive deterioration of song. This model (Fig. 4a) fits with the intuitive idea that the effects of hearing loss simply reveal the nature of changes that develop in the motor pathway for vocal production in the absence of external (feedback-based) guidance.

An alternative possibility is that the mechanisms that evaluate auditory feedback interpret the absence of feedback as ‘incorrect’ feedback, leading to the generation of an error signal that actively instructs changes to song. According to this model (Fig. 4b), a component of song deterioration following deafening is due not to ‘passive drift’ but to ‘active instruction’ by calibration mechanisms that are operating on incorrect information about the quality of song.

Both of these models posit that there is a continuing evaluation of auditory feedback in adult animals. According to a third model, the motor program for learned adult song is normally stable (that is, not subject to biological perturbation that would lead to ‘drift’), and consequently does not require feedback-based calibration. However, this model assumes that deafening has indirect, non-auditory consequences that cause an ‘induced drift’ of the motor program for song (Fig. 4c). For example, as song is important in social interactions,
finch song. They played back a delayed version of the original song that was superimposed on (and consequently disrupted) the auditory feedback that the bird experienced. Over a period of weeks, birds began repeating, adding, altering and deleting syllables, and these changes persisted after the restoration of normal feedback. This experiment showed that it is neither simply trophic consequences of deafening nor the complete absence of feedback that causes deterioration in adult song. Delayed auditory feedback has similar consequences for humans, causing slowing, pausing and abnormal repetitions of phonemes. In humans, these effects are immediate, and are present only while feedback is altered, indicating an acute influence of auditory feedback on vocal production. There is some indication that altered feedback may also acutely disrupt zebra finch song (J. Cynx, personal communication). The experiment of Leonardo and Konishi also shows that the song motor program can be lastingly altered by persistently disrupted feedback.

The deterioration of zebra finch song in response to alteration of feedback is suggestive of an actively driven process. However, this deterioration could in principle have resulted from a process of 'passive drift' (FIG. 4a) because, as in deafened birds, no veridical feedback was available. Likewise, indirect effects of altering feedback, such as increased stress, could have resulted in 'induced drift', although this possibility is less likely because, in one bird, changes to song seemed to be restricted to the single syllable for which feedback was disrupted. The best evidence for active evaluation of auditory feedback in adult birds comes from the gradual recovery of song in these birds following the restoration of normal feedback. This recovery shows that, in some sense, the birds retained a memory of their original song. This memory may be a sensory representation, like the song template, relative to which the disrupted song is compared and recalibrated. However, even after extended exposure to altered auditory feedback, zebra finches with generally disrupted song still produced occasional normal versions of their original songs. Hence, the original motor program for song, although not usually expressed, was nevertheless retained in some form even at the peak of song disruption. This highlights the possibility that the recovery of song could occur independently of feedback evaluation. Suppose, for instance, that disruption of feedback causes physiological changes that obscure the original motor program for song without 'erasing' it (for example by reducing the level of inhibition in the motor pathway and concomitantly increasing the variability of motor production). Then reversal of these changes following restoration of normal experience could lead to a re-expression of the original song, without the necessity of 'recalibrating' the motor program. The data from recovery of song therefore argue that a memory of the original song is retained, but do not determine whether this memory is of the sound of the original song, or of the motor activity required to produce it. Indeed, this would be true even if the birds had never produced normal song while in their deteriorated state.

For humans, there is clear evidence that vocal production in adults is actively matched to internal perceptual targets — subjects exposed to feedback that has been shifted in frequency rapidly and unconsciously shift the frequency of their speech in the opposite, compensatory direction. So, at least for humans, there are brain systems that actively evaluate feedback and keep
vocalizations matched to an internal model. This experiment depends on the use of earphones, and so would be technically more difficult in songbirds. However, if adult songbirds are like humans and adaptively modify their vocal output, experiments in songbirds could enable the characterization of the neural signals underlying this adaptation.

**Neural substrates for song learning**

The behavioural studies of song learning indicate that there must be neural circuitry for a series of processes: memorization of a song template, evaluation of auditory feedback relative to the template, and consequent modification of vocal output. Although song and speech learning evolved independently, the shared requirements of vocal learning in both groups may have led to a related function of brain areas that are not entirely equivalent. So studies of the songbird brain can potentially shed light on general neuronal mechanisms and circuits required for vocal learning. One probable location for many of the neuronal mechanisms underlying song learning is the specialized set of brain nuclei collectively referred to as the song system33,52,53 (FIG. 5). This song circuitry is conventionally subdivided into a 'motor pathway' and an 'anterior forebrain pathway' (AFP). A complex network of forebrain auditory areas provides the crucial auditory inputs to this system42–44 (FIG. 5), but may also be a site of some of the specialized operations critical to song learning.

**Motor pathway for song production.** The motor pathway (FIG. 5) is required throughout life for production of learned song52. This circuit includes HVc and robust nucleus of the archistriatum (RA), which ultimately project to midbrain and brainstem nuclei controlling the muscles of the avian vocal organ (the syrinx) and the muscles of respiration46. Further nuclei afferent to HVc, including nucleus interfacialis (NIf) and nucleus uvaeformis (Uva) are probably part of the motor pathway, but their role is less clear46–49. Neural activity in the motor pathway, particularly in HVc and RA, has been correlated with specific aspects of song structure, and perturbation of this activity disrupts song44,53. It is likely that much of the learned motor program for song is eventually stored in this pathway. The motor pathway could also be involved in the processes of song memorization and feedback evaluation. However, its role in these processes has been difficult to study using traditional techniques such as lesions, because song learning is usually assayed by analysing the vocal motor output of the bird.

**Anterior forebrain pathway.** The anterior forebrain pathway (AFP) (FIG. 5) is a BASAL GANGLIA–dorsal forebrain circuit33,52,53 that is particularly prominent in birds that learn to sing. This circuit is interconnected with the motor pathway42,46,54,55, but is not required for normal production of adult song46–49. However, various studies indicate that this pathway may be critical in song learning. First, lesions of the AFP in young zebra finches prevent normal song learning6–10. Second, pharmacological disruption of normal neuronal activity in the lateral magnocellular nucleus of the anterior neostriatum (LMAN) during tutor song exposure (and not during vocal practice) prevents birds from producing an accurate copy of the tutor song6. This suggests that the AFP participates in song memorization and is potentially a site of template storage. Third, during the course of song learning, neurons in the AFP become more responsive to the sound of the bird’s own song or the tutor song than to most other sounds, including sounds of other individuals of the same species61–63. This selectivity, which probably derives from HVc64,67 (see below), potentially endows the AFP with the capacity to ‘listen to’ and evaluate the bird’s own song relative to the tutor song. Finally, lesions of the AFP interfere with the capacity of adult zebra finches to discriminate between songs, particularly their own song and the song of other birds64,65. This suggests that the AFP may contribute to a fine-grained perceptual analysis of sound. Collectively, these observations have led to the hypothesis that, during song learning, this basal ganglia pathway may participate in memorizing the tutor song and subsequently in evaluating feedback of the bird’s own song and guiding adaptive changes in the motor pathway.

Figure 5 | The song system and its forebrain auditory inputs. Motor pathway nuclei are shown in green, the anterior forebrain pathway (AFP) nuclei in red, and forebrain auditory inputs are grey. The motor pathway, necessary for normal song production throughout life, includes HVc and robust nucleus of the archistriatum (RA). RA projects to the tracheosyringeal portion of the hypoglossal nucleus (nXIIb), which controls the vocal organ, or syrinx, and to nuclei involved in the control of respiration during song22,45. HVc sends a projection to the AFP nucleus Area X (REF. 22), which is homologous to basal ganglia33,52,53. The AFP forms a loop through the medial nucleus of the dorsolateral thalamus (DLM), and the lateral magnocellular nucleus of the anterior neostriatum (LMAN), before returning to the motor pathway at the level of RA44,54,55. Auditory inputs enter the song system at the level of nucleus interauralis (NIf) and possibly HVc, through direct and indirect projections from the Field L complex and from higher auditory areas, such as the medial portion of caudal nucleus of the nissi (NCM) and caudal nucleus of the ventral hyperstriatum (cHV)42–44. NIf projects directly to HVc and may have both sensory and motor functions46,47,49.
In adult zebra finches, lesions of the AFP do not have immediate effects on the production of learned song86,29. However, the AFP seems to be critical in modifications of adult song in response to experimental manipulations87,89,22. For example, lesions of LMAN, which projects from the AFP into the motor pathway (FIG. 4a), prevent the gradual deterioration of song that normally follows deafening21 (FIG. 6). If this deterioration results from ‘active instruction’, then AFP lesions may prevent deafening-induced changes by interrupting the generation or transmission of the putative instructive signal (FIG. 4b). This possibility is consistent with the AFP continuing to play a similar role in adulthood to that hypothesized during song learning: evaluation of feedback and instruction of (normally adaptive) changes in the motor pathway. Alternatively, or in addition, the AFP may function more permissively in motor pathway plasticity — AFP lesions might prevent an instructive signal from driving changes in the motor pathway, or might prevent other sources of disruption (non-instructive perturbation in FIG. 4a,c) from acting on the motor pathway. For example, if song deteriorates following deafening because of unguided addition of new neurons to the motor pathway,21 then lesions of LMAN must specifically block the birth or functional incorporation of these neurons. Either ‘instructive’ or ‘permissive’ interpretations of the function of the AFP in adult birds are also consistent with two other reported effects of LMAN lesions: the prevention of incorporation of new syllables into songs of birds undergoing late learning22, and the prevention of gradual changes to the abnormal songs of adult birds whose motor production has been disrupted by denervation of the syrinx21.

Although the role of the AFP in song plasticity remains unclear, the influence of this pathway on the song motor program is probably mediated in large part by projections from LMAN into the motor pathway at the level of RA22,46,54,55,72 (FIG. 5). Neurons in LMAN project to dendrites within RA that also receive inputs from the motor nucleus HVc21,22. In the context of an instructive role for the AFP, this convergence potentially enables patterned activity from the AFP to shape synaptic function and connectivity within the motor pathway73,74. Alternatively, in the context of a permissive role, neuronal or trophic inputs from the AFP may modulate the capacity for motor pathway plasticity without providing specific guidance. Consistent with the latter possibility, LMAN is known to play a trophic role in supporting development of the motor pathway during early development75–77. Of course, possible instructive and permissive roles of the AFP may be intertwined — modulation of motor pathway plasticity might be integral to mechanisms underlying instructive change. Elucidation of AFP function is likely to benefit both from further investigations of the synaptic mechanisms of interaction between the AFP and motor pathways, and from monitoring and manipulating patterns of activity in the AFP during song learning and in response to alteration of auditory feedback.

The AFP shares homology with mammalian cortical-basal ganglia circuits on the basis of numerous anatomical and physiological considerations90,91,92. The role of the AFP in both juvenile and adult vocal motor plasticity further highlights functional parallels to mammalian systems. Cortical-basal ganglia circuits in mammals are critical for motor control and for motor reinforcement learning93,79. Moreover, as in adult zebra finches, the contribution of such circuitry to motor function in humans and monkeys can be more pronounced during conditions of learning and error correction than during previously learned performance94,90,95.

The nature of instructive signals
We do not yet understand the mechanisms that subserve the evaluation of the bird’s own song relative to a stored song model and the subsequent modification of the song motor program. However, neural responses to song stimuli have been characterized in several parts of the song system and provide some insights into what mechanisms are possible. One intriguing property is ‘song-selectivity’, first described in HVc96,97, but now shown to exist throughout the song system98, including the AFP99. Song-selective neurons respond more strongly to playback of the bird’s own song and, in some cases, the tutor song, than to conspecific songs. Such neurons are
well suited to process auditory feedback of the bird's own song and to participate in evaluating the similarity of that song to the tutor song. For example, neurons that respond selectively to the tutor song would presumably fire more strongly to the extent that auditory feedback of the bird's own song resembles the tutor song, and so could contribute to a signal indicating degree of match. Although we have focused on the possible importance of the AFP to feedback evaluation, the presence of song selectivity in many song nuclei indicates that the mechanisms involved in song memorization and feedback evaluation could be highly distributed or reside elsewhere in the song system. Indeed, some of the specialized auditory processing that subserves song learning may occur in auditory areas that are afferent to the song system. Consistent with this possibility, neurons in the high-level auditory areas, caudal nucleus of the neostriatum (NCM) and caudal nucleus of the ventral hyperstriatum (chV) (FIG. 5), show some aspects of song selectivity in non-anesthetized or sleeping birds, and in some cases are entirely absent85,86. So the strength, and perhaps the nature, of responses to sounds are 'gated' by the behavioral state of the bird. In other systems, sensory responses related to a behavior are 'gated' by the motor activity that generates the behavior87. For songbirds, auditory feedback of the bird's own song is only available and only relevant when the bird is actually singing. This raises the possibility that anesthesia or sleep may artificially open a gate that is normally operated by the act of singing. These results also reiterate the point that an understanding of the mechanisms that participate in the evaluation of auditory feedback may require recording neural activity when that feedback is relevant, namely during the production of song.

Recordings from the AFP of adult birds that are singing and listening to their own songs indeed show that the neural activity during singing is strikingly different from that elicited by playback of the bird's own song87. In particular, the level of activity is much greater during singing than during playback, and a significant portion of this activity seems to correlate with motor production rather than sensory feedback. Activity such as this, which may reflect premotor commands without being required for motor production, is sometimes referred to as 'corollary discharge' or 'efficiency copy'. Such activity may inform sensorimotor structures about the timing and nature of impending movements93. Hence, one possible role for corollary discharge is that song system would be to 'gate' or otherwise inform the processing of auditory feedback.

The presence of corollary discharge during singing complicates the investigation of how auditory feedback is processed, as sensory and motor-related activity may be intermingled in the same neurons both before and after deafening, or with reversible alterations of auditory feedback. An alternative hypothesis about the effects of deafening on the AFP is suggested by the presence of corollary discharge activity in the AFP in waking birds. In other systems, such activity may serve to provide information about the expected sensory consequences of motor commands97. So rather than directly evaluating auditory feedback, the AFP may receive a prediction of expected feedback, perhaps created by the association of premotor signals and auditory feedback in HVc94,95. One advantage of such a model is that it potentially shortens the delay between premotor activity and evaluation of its sensory consequences. If the AFP receives a predictive signal from HVc, this signal may change only slowly, after consistently altered feedback changes the pattern of association between motor commands and auditory feedback. In this case, the gradual deterioration of song following deafening might not reflect the time required to change the motor pathway, but rather the time necessary to update the efference copy prediction.

Finally, the patterned activity in the AFP may not be related to evaluation of song, but may instead relate to other motor or motivational functions of this circuit (BOX 2). Indeed, investigations of AFP function have not clarified so far whether the pattern of activity in this circuit is essential for its role in vocal plasticity.

Conclusions

Behavioural experiments indicate that strikingly similar processes contribute to the learning and maintenance of birdsong and speech. For both birds and human auditory feedback during development is critical in shaping the motor program to produce vocalizations that are matched to the sounds of others. Once learned, adult vocalizations generally remain stable, however, elimination or alteration of auditory feedback in adults shows that neither song nor speech becomes 'hard-wired' and impervious to the influence of experience.
In addition to hearing, there are various non-auditory factors that can profoundly influence song learning and production. Most of these arise from social interactions. During sensory learning, the selection of a song model for eventual imitation by a developing bird does not depend simply on what songs are heard; rather, it is influenced by the degree and quality of social interactions with other birds. For example, live tutors may be more effective than taped songs for some species. Vision is likely to mediate at least part of this social influence on learning. Indeed, young finches visually isolated from an adult tutor may fail to learn their song in spite of normal acoustic contact. Social factors can also shape the final stages of sensorimotor learning. During this period, the mature song that a bird will retain is often selected from a larger and more variable repertoire. Which songs are retained and which are discarded depends not only on how well different variants match a presumptive acoustic target, but also on auditory and non-auditory interactions with other birds. For example, cowbirds will preferentially retain songs that are effective in eliciting visual displays from females that reflect receptiveness to courtship and mating. Similarly, there is an indication that territorial interactions, which rely heavily on ‘counter-singing’ between neighbours, can influence which songs are retained.

In adult birds that have completed learning, there continues to be an influence of social factors on song production. In some species, birds produce more song when singing to others in courtship or territorial contexts (‘directed’ song) than when singing alone (‘undirected’ song), and subtle aspects of song structure may also vary between these two conditions. Interestingly, it has been further shown in adult zebra finches that neural activity in the AFP varies between directed and undirected song. This raises the possibility that signals related to social interactions might also have access to the AFP during development, and that this basal ganglia circuit might mediate the influence of such signals on sensory and sensorimotor learning. One possible source of such signals are midbrain dopamine neurons thought to participate in reward and reinforcement learning in all vertebrates. In songbirds, dopamine neurons project heavily to the song system, especially Area X, and are therefore well situated to provide signals that could modulate or guide song learning.

Although the detailed mechanisms that mediate the influence of auditory feedback on the learning and maintenance of vocalizations remain unknown, parallel studies of birdsong and human speech point to complementary gaps in our knowledge and important directions for future research. For example, it is plausible that the deterioration of both speech and birdsong that is observed following deafening results from ‘drift’ in vocal control structures that accumulates in the absence of correction by auditory feedback. However, the finding that lesions of a basal ganglia circuit can block the deafening-induced changes to song suggests that this song deterioration reflects a more active process. This raises the possibility that active processes might similarly contribute to the deterioration of human speech following hearing loss. A related issue is whether feedback-based mechanisms that keep vocalizations actively matched to a perceptual target are retained in adulthood. In this case, clear evidence for matching to a perceptual target is provided by human experiments in which speech is adaptively modified in response to altered feedback. However, the analogous finding in songbirds has yet to be demonstrated.

Several lines of evidence in juvenile and adult birds indicate that the AFP is involved both in auditory processing of song and in enabling of song motor plasticity. One hypothesis is that these two functions are related; that is, that the basal ganglia circuit evaluates auditory feedback to guide adaptive changes to song. This possibility indicates that it might be informative to examine human basal ganglia and frontal cortical function during adaptation of speech to altered feedback. Alternatively, the AFP may play a trophic, permissive role in vocal plasticity. Either way, basal ganglia circuitry is required for modification of vocal output; thus, humans with basal ganglia dysfunction, such as occurs in Parkinson’s and Huntington’s diseases, might have difficulty in modifying speech to compensate for altered feedback.

In songbirds, observation and manipulation of behaviour can be coupled with recording and disruption of neural activity. Future studies in this system therefore have the potential to elucidate the mechanisms involved in the feedback-based calibration of vocal production. In particular, it may be especially informative to further characterize the types of neural signals present in the AFP during periods of song learning and adaptation of song to altered feedback. A better understanding of the role of cortical–basal ganglia circuitry in birdsong and speech has the potential not only to clarify how auditory feedback contributes to the calibration of vocal production, but also to reveal general mechanisms that underlie performance based motor learning.

FURTHER INFORMATION Allison Doupe’s laboratory: Recoding the bird’s song

ENCYCLOPEDIA OF LIFE SCIENCES Bird song: steroid hormones and plasticity


A key question is whether song-selectivity reflects the tutor song or the bird’s experience of its own voice. This work tackled the issue for AFP neurons by studying birds induced to sing songs very different from their own. This indicates that although the bird’s own song is required, but many of them also respond to the tutor song. Therefore both the bird’s own song and tutor song experience seem to shape the properties of these nuclei.


57. Marples, D. A. Contributions to the understanding of the evolutionary relationship of these vocal areas to structures controlling vocal birds and in mammals bearing homologous nuclei.


31. Nordeen, K. W. & Nordeen, E. J. Projection neurons within a discrete system would bias the study of vocal learning, and delineated many of the questions that still occupy the field, including the localization of auditory and motor song memories, the interhemispheric coordination of vocalization and the evolutionary relationship of these vocal areas to structures controlling vocal birds and in mammals bearing homologous nuclei.


29. Nordeen, K. W. & Nordeen, E. J. Projection neurons within a discrete system would bias the study of vocal learning, and delineated many of the questions that still occupy the field, including the localization of auditory and motor song memories, the interhemispheric coordination of vocalization and the evolutionary relationship of these vocal areas to structures controlling vocal birds and in mammals bearing homologous nuclei.


13. Deafening in adult zebra finches reduces the rate of neuronal replacement in the HVC. The authors point out that it remains unclear whether these changes are dependent on the loss of auditory feedback per se or on indirect consequences of deafening. Nevertheless, the results illustrate that deafening can induce profound changes in the neurophysiological processes underlying song production.


REVIEWS


91. Schmidt, M. F. & Konishi, M. Gating of auditory responses in the field L complex, which is one of the sources of auditory input to HVC. Such 'gating' of auditory input to a vocal control nucleus may reflect the regulation of sensory feedback signals generated by an animal's own movement. J. Neurosci. 16, 265–297 (1993).


Acknowledgements

We thank S. Lisberger for helpful comments on the manuscript. The work of the authors was supported by the National Institutes of Health, a Burroughs Wellcome Fund Fellowship of the Life Sciences Research Foundation, the John Merck Fund and the E JLB Foundation.