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Song learning in birds: the relation between perception and production

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SUMMARY

The vocal control system of oscine songbirds has some perplexing properties – e.g. laterality, adult neurogenesis, neuronal replacement – that are not predicted by common views of how vocal learning takes place. Similarly, we do not understand the relation between the direct pathway for the control of learned song and the recursive pathway necessary for song learning. Some of the paradoxes of the vocal system of birds may disappear once the relation between the perception and production of learned vocalizations is better understood. To some extent, perception and production may be two closely related states of a same system.

1. INTRODUCTION

Vocal learning in birds raises questions that address basic issues of brain function. For example, why is there a functional asymmetry in pathways for vocal learning and how is it represented? The left half of the song system in canaries plays a dominant role in song production (Nottebohm *et al.* 1976; Nottebohm 1977) despite neuroanatomical (Nottebohm *et al.* 1981) and electrophysiological (McCasland & Konishi 1981) equivalences between the two sides. Why do some songbirds learn to produce more songs than they use in their adult repertoire (Marler & Peters 1981)? Why do the muscles of the syrinx respond to sound (Williams & Nottebohm 1985)? What causes neurogenesis to occur in some parts of the adult song control system (Goldman & Nottebohm 1983; Paton & Nottebohm 1984)? How does this neurogenesis relate to functional needs of the adult brain (Nottebohm 1989)? How do birds perceive song? A common theory of song learning in birds – first memorize a model, then modify vocal output until the model is matched – does not answer the above questions. We suggest that there is a close relation between how a bird learns to produce its song patterns and how it perceives conspecific song, and that this relation may hold the answer to some of the riddles posed by the vocal control system.

We report here on three separate studies that may shed light on the relation between song production and song perception. These studies focus on: (1) neurogenesis in a song control nucleus; (2) the relation between learning and forgetting, and (3) how song is perceived.

We present data from work done with two songbird species: the zebra finch and the canary. Both acquire their song by reference to auditory information (Immelmann 1969; Marler & Peters 1977). They

differ in the timing of their song learning: it occurs during the juvenile stage in zebra finches (Immelmann 1969) and during juvenile and adult life in canaries (Nottebohm & Nottebohm 1978).

2. CIRCUITS FOR THE CONTROL OF LEARNED SONG AND SONG LEARNING IN CANARIES AND ZEBRA FINCHES

Figure 1 presents a partial sketch of the song system, which presides over song and other learned vocalizations (Simpson & Vicario 1990). This system is composed of anatomically discrete areas which we call ‘nuclei’. Fibre pathways connect these nuclei. Neurons that make connections only within a nucleus are called ‘interneurons’; neurons that send fibres – axons – to another nucleus are called ‘projection neurons’. The gross anatomy of the song system – similar in canaries and zebra finches – shows few right–left differences; the connections shown in figure 1 are all ipsilateral. There are some contralateral connections between thalamic nuclei of the song system (Nottebohm *et al.* 1982; Williams 1985*a*) but they are not shown here. The names of each of the song control nuclei, and their abbreviations, are shown in the legend to figure 1. The high vocal centre (HVC), robust nucleus of the archistriatum (RA) and tracheosyringeal component of the hypoglossal nucleus (nXIIts) are necessary for the acquisition and expression of learned song (Nottebohm *et al.* 1976); area X and lateral magnocellular nucleus of the anterior neostriatum (LMAN) are important for song learning but are not necessary for the production of learned song (Bottjer *et al.* 1984; Scharff & Nottebohm 1989; Sohrabji *et al.* 1990).

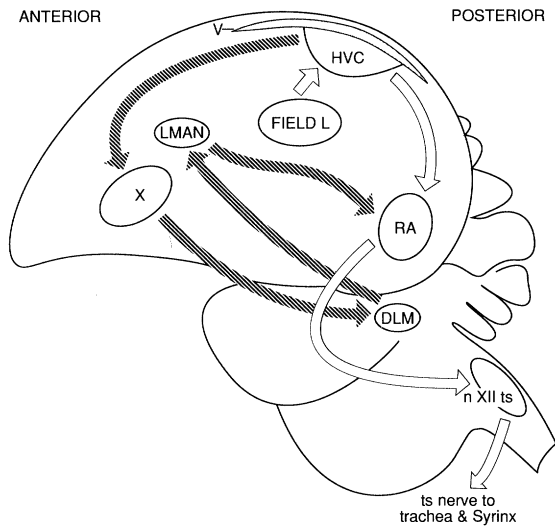


Figure 1. Partial sagittal sketch of the song system of songbirds. The HVC-RA-nXIIts circuit is the backbone of the motor pathway for the control of learned song. The HVC-area X-DLM-LMAN-RA recursive loop is important for song learning. Field L provides the auditory input to HVC. Abbreviations: HVC, high vocal centre; RA, robust nucleus of the archistriatum; nXIIts, tracheosyringeal part of the hypoglossal nucleus; DLM, medial portion of dorsolateral thalamic nucleus; LMAN, lateral part of the magnocellular nucleus of the anterior neostriatum; V, lateral ventricle.

3. THE GENESIS OF RA-PROJECTING NEURONS OF THE HVC AND ITS RELATION TO STAGES IN SONG LEARNING

About 50% of the HVC neurons of the adult zebra finch and canary brain project to the robust nucleus of the archistriatum (RA), which is part of the efferent pathway for song control. Approximately 25% of HVC's neurons project to area X. The remainder of HVC neurons (25%) are interneurons (A. Alvarez-Buylla & F. Nottebohm, unpublished observations).

Most of the canary HVC neurons that project to area X are born before hatching; very few are added thereafter (Alvarez-Buylla *et al.* 1988; Gahr 1990). The converse is true for canary HVC neurons that project to RA (figure 2). Very few of these neurons are born *in ovo*. RA-projecting HVC neurons are first produced in significant numbers after hatching (counted at sexual maturity), with a peak around day 10 (0.9% per day). The rate of production during the next 40 days drops to 0.55% per day; it remains relatively high, somewhere between 0.4 and 0.6 until day 240 and drops to 0.15% by the end of the first year. The daily percentage of new RA-projecting neurons added to HVC in October, when the birds are about 15 months old (0.4%) is comparable to that added during post-natal development; however, this is probably a temporary peak. Subsequent months show a lower rate of labelling of RA-projecting neurons, with a second, smaller peak in February (0.25%) (Alvarez-Buylla *et al.* 1988 and unpublished results).

Canary subsong starts at about 40 days of age (Nottebohm *et al.* 1986). By that time less than one fourth of HVC's RA projecting neurons have been generated and many of these cells may not yet have differentiated or innervated RA. Subsong in zebra finches begins as early as day 28 (Arnold 1975), when the innervation of RA by HVC neurons is commencing (Konishi & Akutagawa 1985); at this time new RA innervating neurons are still being born and recruited into HVC (Nordeen & Nordeen 1988). Stimulation of NXIIts from HVC in male zebra finches is not yet possible at that time (H. Williams, unpublished observations), presumably because the link between HVC and RA is not sufficiently established. Thus in canaries and zebra finches song development starts when HVC is just starting to gain control over RA and its caudal projections. Thereafter song development probably reflects changes in all of the nuclei and pathways shown in figure 1, including a sustained development of the HVC-RA link.

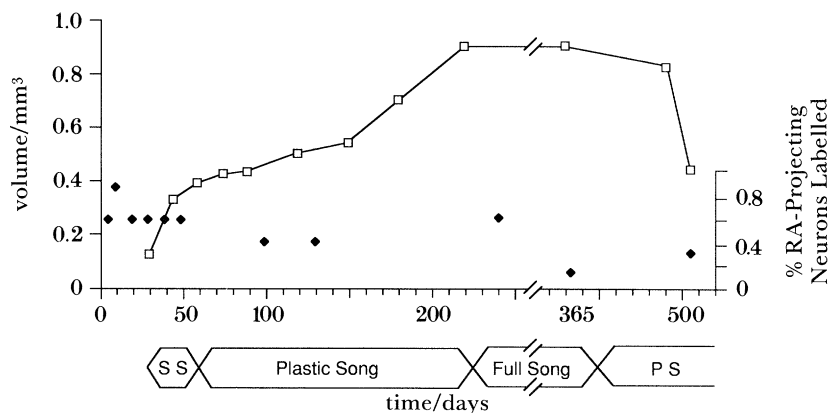


Figure 2. The genesis of HVC RA-projecting neurons and its relation to HVC growth and to stages in song learning in male canaries. HVC volume in cubic millimetres, as defined by Nissl stain (open squares) increases during development, remains stable during the breeding season, then crashes as the breeding season comes to a close and the birds start to molt (from Nottebohm *et al.* 1986, but see Gahr 1990). The solid diamonds (two to five birds per sample point) show the percentage of HVC's RA-projecting neurons labelled per day of [³H]thymidine treatment at each of the post-hatching ages (in days) indicated. Birds injected between 5 and 240 days after hatching were sacrificed at 400 days of age and some of the labelled neurons could have died before then (from Alvarez-Buylla *et al.* 1988). Birds injected at 365 and 500 days were killed 125 days after the last injection (Alvarez-Buylla *et al.*, unpublished observations).

Eighty percent of the song syllable types that a male canary produces at sexual maturity (8 months) are present by the end of the fourth month, though rendered in an unstable manner (Nottebohm *et al.* 1986). By that time HVC has less than the full complement of RA-projecting neurons present at maturity and many of these cells may not yet have differentiated and formed connections. Thereafter a few more syllable types will be added and the whole repertoire will become stereotyped. Thus canary song emerges as a learned motor skill at the time the pathway from HVC to RA is laid down (Alvarez-Buylla *et al.* 1988). The addition of neurons to HVC – RA-projecting and interneurons – during the last 3–4 months of song development may be related to increases in the stereotypy of sounds produced or to other functions, such as perception, and these roles need not be mutually exclusive (more on this later). The addition of new neurons to the canary HVC does not stop at song crystallization; it continues into the breeding season (figure 2). New neurons also continue to be added to the HVC of adult zebra finches (Nottebohm 1984; Nordeen & Nordeen 1988). In both canaries and zebra finches a significant fraction of the HVC neurons added in adulthood project to RA (Alvarez-Buylla & Nottebohm 1989).

At the end of the breeding season the song of male canaries becomes unstable and many new – also unstable – syllables appear then for the first time. At that time HVC, as defined by Nissl stain, shrinks in volume (Nottebohm 1981) with an apparent loss of 38% of its neurons (Nottebohm 1985). Part of this effect may be attributable to staining changes that reflect changes in cell activity, leading to an apparent displacement of HVC's ventral boundary (Gahr 1990). The apparent reduction in HVC neuronal numbers is accompanied or followed by increased neurogenesis, including a resurgence in the formation of new projection neurons (Kirn & Nottebohm 1989; Alvarez-Buylla & Nottebohm 1989). Soon after song regains its stereotypy (Nottebohm *et al.* 1986). The volume of HVC as defined by Nissl stain during the breeding season is comparable at 1, 2 and 3 years of age (Nottebohm *et al.* 1981). From this we infer that the neurogenesis that occurs in adult HVC is accompanied by the replacement of older neurons which presumably die. We do not yet know what is the time lag between the death of an HVC neuron and its replacement and whether this time lag changes seasonally. In principle there need be no time lag: a new neuron could help hasten the demise of the neuron it replaces.

It is tempting to relate neurogenesis in HVC to processes of song learning. Yet we do not know how song learning occurs. Perhaps an auditory memory of song is first acquired and thereafter vocal output is modified until the feedback it generates matches the model. This interpretation is supported by the observation that deafening before song acquisition as a motor skill invalidates the effects of exposure to a model (Konishi 1963; Nottebohm 1968). However, new facts suggest other possible mechanisms, also affected by early deafening. Auditory input stimulates neurons in HVC (Katz & Gurney 1981), RA and

nXIIIts, at least in adulthood; sound responses in RA and nXIIIts disappear if HVC is removed (Williams & Nottebohm 1985). Auditory stimulation also affects the firing of neurons in area X and LMAN (Doupe & Konishi 1989). Sound stimulation could affect the formation and survival of synapses in each of these nuclei. Sound inputs could also regulate the birth, differentiation and survival of new neurons in some of these nuclei, as suggested for neurogenesis in adult HVC (Bottjer & Dignan 1988). If such effects occurred during ontogeny, then song stimuli – or even sounds in general – could have a direct effect on the ontogeny of song motor pathways and of the patterns they control. The devastating effects of early deafening on the song quality of oscine songbirds could result from both the lack of access to auditory models and from the absence of auditory input to the song control pathways. These two effects may interact in interesting ways.

A test of the direct effects of sound on vocal ontogeny has not yet been made. Some HVC neurons are responsive to sound in juvenile birds but the context, extent and time of onset of such responses have not been described in detail (Volman & Konishi 1987). We know that zebra finches imitate sounds heard during the first 35 days after hatching (Böhner 1990); during the last 10 days of this period song stimuli could influence the emerging connections of the song control system, including the link between HVC and RA.

HVC, RA, nXIIIts and the indirect pathway linking HVC to RA, area X, the medial portion of the dorsolateral thalamic nucleus (DLM) and LMAN, are perhaps involved not just in song acquisition as a motor skill but also in song perception. Song perception affects several behaviours, such as song learning, countersinging, recognition of territorial boundaries and pair formation. Song stimulation induces nest building and ovulation in female canaries (Kroodsma 1976). HVC seems to regulate this effect in a still poorly understood manner. Bilateral HVC lesions increase nest building and shorten the latency to ovulation (Greenspan & Ingram 1983). An intact HVC, in the absence of song input, may inhibit female reproductive behaviour. Song stimulation of HVC – or HVC's outright removal – may lift this inhibition. A perceptual involvement by HVC might explain why neurogenesis in adult canary HVC occurs in both male and female canaries (Paton & Nottebohm 1984; Nottebohm 1985) even though females sing less and their repertoire is smaller and less stereotyped. Perhaps there are two kinds of neurogenesis in HVC, one related to the laying down of perceptual memories – a process common to young and adult male and female canaries – the other one related to acquisition of the motor skill, including stereotypy, a process that would be in evidence, particularly in males. We do not know if these two processes would involve the same type or types of neuron.

HVC neurogenesis occurs in adult male zebra finches at daily rates that are somewhat higher than those seen in adult male canaries in reproductive condition (0.09 and 0.06% respectively) (Alvarez-Buylla *et al.*, unpublished observations). However, the rate of production of new RA-projecting neurons differs markedly between

the two species. Whereas 56% of all neurons produced in adult canary HVC project to RA, only 23% of all neurons produced in adult zebra finch HVC do so (Alvarez-Buylla & Nottebohm 1989). We know that both species differ in their ability to produce new songs in adulthood, but we do not know if they differ in their ability to recognize and remember new songs.

It has been suggested that in the swamp sparrow most of the neurons in HVC and area X are generated during the early period of sensory learning. Song models are committed at this time to sensory memory, but few models if any are added during the period of motor learning which in this species occurs later. Therefore recruitment of new neurons may relate to the acquisition of sensory, but not motor memories (Nordeen *et al.* 1989). However, this information is based on neuronal counts, not on counts of cells with a known birth date. What seems like a steady state in neuronal numbers during the period of motor learning could be underlaid by neurogenesis and neuronal replacement. Neurogenesis also occurs in area X of adult canaries (F. Nottebohm, unpublished observations), where it may be related to continuing processes of song learning.

4. SONG FORGETTING AFTER BILATERAL LMAN LESIONS

HVC projects to area X, which in turn sends a projection to nucleus DLM of the thalamus. DLM projects to LMAN, and LMAN innervates RA (Nottebohm *et al.* 1976, 1982; Okuhata & Saito 1987; Bottjer *et al.* 1989) (figure 1). Williams (1989) calls this circuit the 'recursive loop', the long way to go from HVC to RA. This recursive loop is not part of the main efferent pathway for the production of learned vocalizations, as shown by the fact that bilateral destruction of LMAN in adult zebra finches does not affect learned song. However, the same lesion in juvenile birds prevents normal song development and the imitation of external models (Bottjer *et al.* 1984).

There are some observations on the mode of action of the recursive loop in adult anaesthetized zebra finches. A sound stimulus arriving at HVC elicits a response in RA with a delay of approximately 10 ms. The delays between DLM and LMAN and between LMAN and RA are much briefer (2 ms). It is possible that a signal arriving at HVC could work its way to RA in about the same time whether it used the direct path or the recursive loop. Upon arrival, these two signals could interact (be 'compared' (Williams 1989)). This comparison may occur in RA's type IV neurons which receive input from both HVC and LMAN (Canady *et al.* 1988).

The direct and recursive pathways differ in the extent to which a signal is amplified. Electrical stimulation of HVC in adult zebra finches elicits a very robust response in RA: there has been signal amplification. Electrical stimulation of LMAN elicits a much smaller response in RA and this response is narrowly defined in time and involves fewer units. Furthermore, electrical stimulation of HVC can drive nXIIIs but electrical stimulation of LMAN cannot. The latter

observation suggests that the auditory driving of nXIIIs results from stimulation of the direct HVC-RA pathway, and not of the recursive loop (Williams 1989). However, the test of this hypothesis, snipping the connection between LMAN and RA and then seeing if nXIIIs can be driven by sound, has not yet been done.

The responses of single units to sound suggest that the recursive pathway can extract very specific song information. Units in area X respond to a broad array of auditory stimuli. Units in LMAN respond selectively to presentations of the bird's own song (Doupe & Konishi 1989). However, as units of the latter type have also been reported for HVC (Margoliash 1986), the recursive pathway would seem to recreate information that was already available. Perhaps the selectively responding HVC units project to RA, and the recursive loop repeats this process starting from the X-projecting HVC cells and using somewhat different parameters. We are probably staring at the principles of how a circuit for vocal imitation has to be organized. We now report about the result of lesioning LMAN in adult canaries, with some thoughts about the relation between learning and forgetting.

Adult male canaries deafened after they learned their song, forget it. Their song gradually degenerates until it becomes similar to that of a bird deafened before the onset of song learning (Nottebohm *et al.* 1976). Zebra finches deafened in adulthood retain their learned song (Price 1979). Unlike zebra finches, adult canaries need auditory feedback to maintain the vocal skill they have acquired. In this sense – and also because of the new syllables they continue to add – male adult canaries are constantly relearning their song. This may be a feature of some 'open ended' learners: new songs can be learned because previously learned motor patterns have not cast the efferent pathways into immutable motor programmes.

We speculated that if LMAN is important for song learning during development, its bilateral destruction in adult canaries would lead to a steady deterioration of learned song, and no new learned components would replace the forgotten ones. The outcome of this experiment, done with six adult males, confirmed our expectation (figure 3). Over a period of weeks and months following LMAN lesion in mid-September, syllable diversity dropped dramatically. As this effect became more marked, starting soon after the lesion, birds produced longer and longer phrases of some of the surviving syllables, which also underwent gradual change (F. Nottebohm *et al.*). Interestingly, the song of LMAN-lesioned canaries has features, such as the very long phrases, that have not been observed after deafening (Güttinger 1981). From this we infer that the results of LMAN lesions are different from those that follow interdiction of access to an auditory model.

We do not know if loss of learned song following bilateral LMAN lesion occurs because: (1) these birds cannot use auditory feedback from their own vocalizations to guide song maintenance and song learning (this would be comparable to deafening); (2) they fail to perceive any song, including feedback from their own vocal output, as relevant to their own vocal

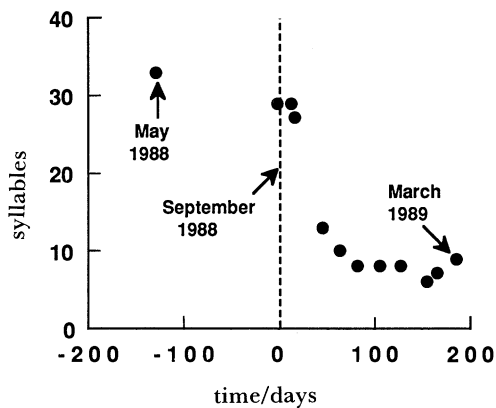


Figure 3. Song loss after late summer bilateral lesions of LMAN (vertical broken line) in an adult male canary. The amount of song recorded for each data point varied between samples; 600 s of song are considered necessary for a complete count of syllable types, but not all samples were that long. From left to right sample lengths (in seconds) were as follows: 623; 74; 238; 192; 725; 600; 650; 512; 507; 341; 350; 626. Data for each point were obtained over a period of 2–3 days. The greatest drop in syllable diversity occurred between the recording of October 3 (two weeks after the operation) and October 31.

behaviour; (3) destruction of LMAN deprives RA from a phasic or tonic input which is necessary for the expression of learned song programmes (a retrieval problem that could account for the very long phrases); or (4) LMAN plays some other role in the acquisition, maintenance and expression of learned vocal programmes. These roles need not be mutually exclusive. Whichever the explanation, the brief survival of song syllables that follows the destruction of LMAN and their disappearance thereafter constitute a process of ‘forgetting’ that will be most interesting to explore.

5. SONG PERCEPTION IN ADULT ZEBRA FINCHES

Birds make important decisions based on differences between the sounds they hear. Sound playbacks under natural or semi-natural conditions can identify what properties of song are responded to. Some studies have focused on the responses of male songbirds to song (e.g. Baker *et al.* 1981 *a*; Baker & Cunningham 1985; Brooks & Falls 1975; Emlen 1972; Falls 1963; Falls & Brooks 1975; Falls *et al.* 1982; Milligan & Verner 1971; Morton 1982; Peters *et al.* 1980; Petrinovich & Patterson 1981; Searcy *et al.* 1982; Weeden & Falls 1959). Others have dealt with female responses to song (Baker *et al.* 1981 *b*; King & West 1977, 1983; Kroodma 1976; Searcy & Marler 1981, 1984; Searcy *et al.* 1981; West & King 1988; West *et al.* 1981). Either approach, however, can only use sounds that elicit overt responses. Lack or diminution of responsiveness by some individuals, by one sex, or at different times of the breeding cycle (e.g. Petrinovich *et al.* 1976) could depend on motivational variables and not necessarily on the way in which sounds are perceived. We have chosen to use operant conditioning techniques to study song perception in the laboratory. Operant techniques

have been used previously to ask birds questions in auditory psychophysics (Dooling 1982, 1986; Okanoya & Dooling 1988) and to explore the cognitive properties underlying sound perception (Cynx & Shapiro 1986; Dooling *et al.* 1987; Hulse *et al.* 1984).

(a) Operant conditioning

Birds presented with either of two sounds broadcast over a same speaker had the choice of perching on a small perch in front of a food dispenser (this was the ‘go’ response) or not doing this (the ‘no go’ response). Correct responses were reinforced by food availability in the food dispenser. Errors were punished by turning off the lights in the testing cage for 15 s. Some of the results we report come from work still in progress.

(b) Self reference

Adult male zebra finches were taught to discriminate between two zebra finch songs. Acquisition of the discrimination was faster if one of the songs was the bird’s own and the other one belonged to another colony male. If the two songs were familiar, but neither was the bird’s own, the number of trials required was considerably greater. If both songs were unfamiliar and unlike the bird’s own, then still more trials were required (figure 4). One interpretation is that song discrimination is centred around the bird’s own song. As the acoustic properties of other song exemplars fall further and further away from self-song, discrimination between these exemplars becomes proportionately harder (J. Cynx and F. Nottebohm, unpublished observations). Observations on how free-ranging songbirds respond to playbacks of their own or another bird’s song (Krebs *et al.* 1981; Morton 1982) or dialect (Milligan & Verner 1971; Baker *et al.* 1981) indicate that differences between self-song and other stimulus songs are perceived. The perceptual world of conspecific vocal signals may bear little resemblance to a sound-spectrographic representation; instead, signals may be classified by kinds and degrees of resemblance to self-song. A same signal may be perceived differently depending on whether the receiver can or cannot



Figure 4. Number of trials to criterion by three adult zebra finch males discriminating between self-song and another familiar song (SELF), between two familiar songs (AVIARY), and between two unfamiliar songs (ALIEN).

produce it, much as speakers who lack experience in the production of 'l' and 'r' sounds are said to be unable to distinguish between them. Margoliash (1986) has shown that some neurons in HVC respond precisely in this manner, giving their strongest response to playbacks of the bird's own song. It would be interesting to know whether birds such as the swamp sparrow, that learn more songs that they produce in adulthood (Marler & Peters 1981), respond selectively to songs they had mastered but no longer sing. Songs learned and subsequently discarded from the repertoire may affect perceptual idiosyncrasies. The need to acquire particular perceptual biases may also underlie song learning in some female songbirds whose song, otherwise, is not known to serve a biological function.

(c) Timbre perception and gender differences

We also wanted to test perception using less complex natural stimuli, and wanted to change these stimuli one parameter at a time. For this we used single zebra finch song syllables. Zebra finch song syllables often include stacks of harmonically related frequencies, henceforth referred to as 'harmonics'. Zebra finches can selectively emphasize or dampen different harmonics of a same syllable (Williams *et al.* 1989). We wanted to know whether such timbre differences could be used to discriminate between sounds used in an operant task.

We tested our birds with two versions of the same syllable: the second harmonic was absent in one, and the fifth harmonic was absent in the other one (figure 5). Adult male and female zebra finches solved the problem by focusing on the presence or absence of the second harmonic. However, these birds took thousands of trials to master the task. Interestingly, though, whereas male zebra finches could use the absence of the

second harmonic either as a 'go' or 'no-go' signal, females were much slower than males in learning to use the absence of the second harmonic as a signal to approach the feeder. This gender difference in behaviour need not be related to how the signal is perceived, but could result from the extent to which perceptual information is available for different functions, in this case a 'go' operant response. It is known from other systems that information that is perceived and integrated into some behaviours may not be available for others (e.g. Konorski 1967; Dobrzecka & Konorski 1968).

(d) Importance of acoustic context

Zebra finches asked to solve the problem of the missing harmonic learn the operant response much faster (1200–1800 trials instead of 6000–20000 or more) if the syllable is embedded in a whole song. In this case the two test stimuli differ only in the presence or absence of the second harmonic in the embedded syllable (figure 5). We do not know whether this improvement in performance occurred due to perceptual salience – e.g. song-embedded syllables engage special processors or elicit increased attention – or because discriminanda presented in this manner are more easily linked to the operant response required by our test, like Konorski (1967). Whatever the reason, the presence of whole song as a context in which to learn the discrimination dramatically improved learning.

(e) Laterality

We wanted to know whether both hemispheres of the songbird brain process song signals in the same way. To do this we destroyed the right or left thalamic

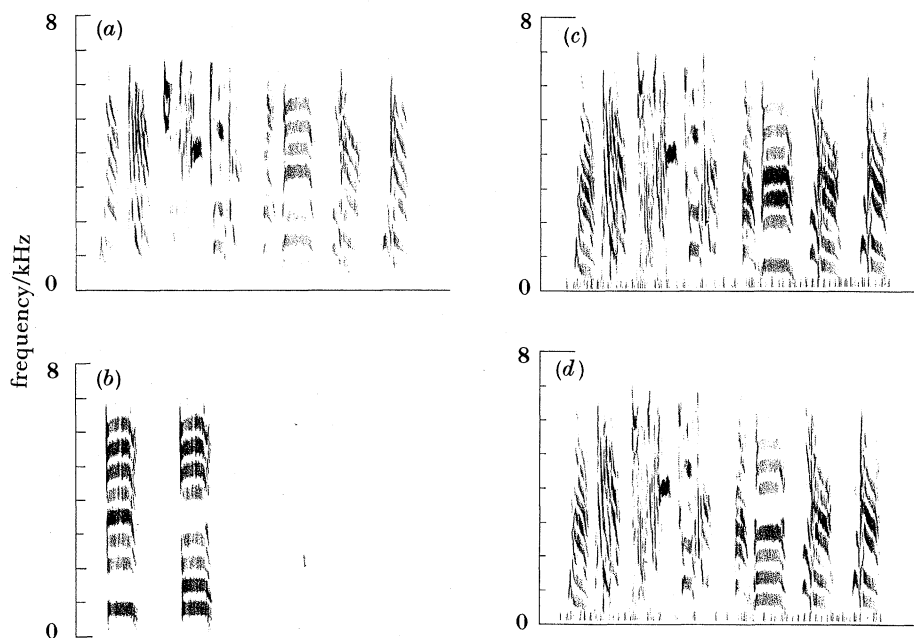


Figure 5. The missing harmonic test: (a) example of adult zebra finch song, (b) syllable (from (a)) with either the second or fifth harmonic missing; (c) and (d) test stimuli with either the second or fifth harmonic missing embedded in songs otherwise similar to (a).

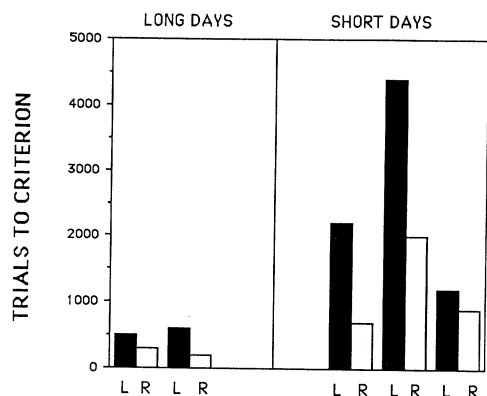


Figure 6. Effects of lesioning the right or left ovoidalis on a song discrimination task. Birds were tested in pairs and had to discriminate between their own song and that of the other member of the pair. All training took place after lesioning. The vertical axis shows number of trials until the discrimination was mastered. Two of the pairs were trained during the summer (LONG DAYS), the other three during the winter (SHORT DAYS).

auditory relay nucleus (nucleus ovoidalis) in adult male zebra finches. Each ovoidalis projects to field L of the ipsilateral neostriatum (Kelley & Nottebohm 1979; Katz & Gurney 1981), which in turn projects to HVC. Removal of one ovoidalis deafens the ipsilateral HVC. This operation does not affect the song of adult zebra finches but it affects their performance in song discrimination tests. Right-ovoidalis-lesioned birds took longer than left-ovoidalis-lesioned birds to recognize the missing harmonic in the song-embedded syllable (figure 6). However, if the same birds were asked to discriminate between two familiar songs, one of them their own, then right-ovoidalis-lesioned birds mastered the task much faster than their left-lesioned counterparts. Perhaps in zebra finches the left hemisphere is better at discriminating between stimuli that differ in many ways ('holistic' perception) and the right hemisphere is better at discriminations requiring a more 'analytic' processing of input. Inter-hemispheric perceptual differences of this type have been reported in humans (Levy-Agresti & Sperry 1968).

(f) Seasonal differences

The experiments on zebra finch song perception described here were done during the spring and summer. Seasonality turned out to be an important variable. Our zebra finches are kept indoors but follow the New York State photoperiod. Much to our surprise we found that learning to discriminate between familiar songs or between songs that differ in the embedded syllable in our laterality experiments took much longer during the winter than during the summer. We do not yet know why this is the case, but possibly environmental factors such as day length and relative humidity affect the gonads and hormonal levels, which in turn may affect brain mechanisms used in the tasks described. Seasonal changes in song perception might be even more marked in strongly seasonal birds, such as the canary, red-winged blackbird and rufus-sided towhee in which some or all of the following song control nuclei – HVC, RA, area X and

nXIIIts – seem to show marked seasonal changes in volume (Nottebohm 1981; Kirn *et al.* 1989; Brenowitz *et al.* 1989). Canaries and red-winged blackbirds can change their song on subsequent years, but this does not happen in rufus-sided towhees. In the latter case seasonal changes in the anatomy of song control pathways may reflect a concurrent need to up-date perceptual memories, perhaps old memories and the cells that encode them are sloughed off, then replaced.

6. OVERVIEW

We do not know yet how learned sounds are processed and whether conspecific sound signals, such as song, receive special treatment. We do not know how and where learned sounds are stored. Does learning permanently and exclusively tie up the neurons and circuits that hold the memories, to the exclusion of other information that therefore cannot be learned? Our earlier observations on sound responses in the motor pathway for the production of learned song (Williams & Nottebohm 1985) suggest that the distinction between sensory learning and motor learning, or between perception and production may not be an easy, or even a necessary one. When dealing with learned vocalizations in humans (Liberman *et al.* 1967; Liberman 1982) or birds both kinds of processes may blur into each other.

The syrinx receives afferent innervation (Bottjer & Arnold 1982, 1984). When the syringeal muscles of songbirds respond, silently, to sound (Vicario 1986), these responses may influence sound perception. Of course, sound activated vocal pathways could also influence perception via more central reafferent pathways. These functional speculations remain untested. Untested too is the suggestion that genesis of new HVC RA-projecting neurons in adulthood serves song perception and the updating of song perceptual memories (Nottebohm 1989).

Different songbirds – chaffinch, canary, white-crowned sparrow and Java sparrow – show left-side dominance for the control of learned song (Nottebohm 1971, 1977; Nottebohm & Nottebohm 1976; Seller 1979). Understanding the rationale behind such a phenomenon, i.e. why it evolved, remains a daunting challenge. Part of the explanation might come from understanding what functions, e.g. different kinds of feature extraction, attentional processes, or production and perception, are simultaneously compatible within a same hemisphere. Other functions, such as decision making, may also require that one hemisphere exert dominant control. Discovering a relation between patterns of laterality in the production and perception of learned song could offer a major breakthrough in our understanding of brain functional asymmetry. Hence we are very excited by the seeming hemispheric asymmetries, preliminary though they might be, in how zebra finches perceive song. Zebra finches have less marked asymmetry in song production (F. Nottebohm, unpublished observations) than canaries. Perceptual asymmetries in canaries might be even more marked.

We may also expect a difference between male and female song perception, particularly in species such as the zebra finch, in which the brain pathways for the control of learned song are less developed in females than in males (Nottebohm & Arnold 1976; Gurney 1981; Konishi & Akutagawa 1985; Williams 1985; Simpson & Vicario 1990). Preliminary data suggest that this is so. Female zebra finches require more trials than males to discriminate between two different zebra finch songs (Cynx & Nottebohm, unpublished data).

The song system of an open ended learner such as the canary shows marked seasonality in anatomy and performance. In canaries one might expect to find seasonal differences in how song is perceived. It surprised us to find seasonal differences in song discrimination in zebra finches, which are usually represented as opportunistic breeders and whose biology, therefore, is thought to be less ruled by day length; their song as a learned pattern does not change between times of year. However, it is known that the song system of zebra finches has many hormone sensitive cells (Arnold *et al.* 1976) and that amount of singing is related to hormone levels (Pröve 1974; Arnold 1975). If blood levels of gonadal hormones change with season and if these changes affect the circuits used in song production, then they may also affect song perception.

The effects of lesioning LMAN and area X on song learning remain unexplained as neither nucleus is on the efferent path used for song production in adulthood. Aberrant song development following LMAN or area X lesions may result from perceptual deficiencies. However, we cannot yet rule out the possibility that area X and LMAN play a motor role during song development.

Auditory input reaches HVC via the ascending auditory pathway (Kelley & Nottebohm 1979; Katz & Gurney 1981). Auditory access to HVC may develop during song learning and may bear a specific relation to the sounds the bird is learning to produce (Volman & Konishi 1986, 1987). Yet, it has been suggested that the auditory feedback a bird generates when singing cannot reach nucleus HVC because of an inhibition of auditory activity in HVC during and for several seconds after song production (McCasland & Konishi 1985). If true, this poses some problems. If HVC is the pattern generator for the fine details of song – a plausible assumption – then how does it know when a model has been matched? The ascending auditory pathway could detect mismatches between the auditory model a bird set out to imitate and the auditory feedback created by its own song. Information about mismatches between model and output could be passed on to HVC, but with a negative sign, thus discouraging the repetition of ‘mistakes’. As long as the bird can hear its own correct feedback, as would be the case during production of stable adult song, pattern generating circuits in HVC may continue to fire unaffected by other environmental sounds. The observations of McCasland & Konishi (1985) are intriguing in other ways, because they report that motor inhibition of auditory activity in HVC lasts for many seconds (e.g. 14 s) after song termination. The

behavioural significance of this observation remains unknown.

One of the most challenging observations ever made about song learning was that male songbirds are predisposed to learn some songs but not others (Thorpe 1958; Marler 1970), and female songbirds respond preferentially to conspecific song (King & West 1977; Searcy & Marler 1981; Searcy *et al.* 1981; Searcy & Marler 1984; West & King 1988). The source of these predispositions is a mystery. The same songs that are accepted as models by juvenile males are used in adulthood to repel trespassing males and to attract and seduce females. Parsimony might lead us to argue that the same features make song effective in each of these functions, and that therefore juveniles and adults of both sexes perceive these features in an equal manner. And yet, the processes of perception leading to a preference for a same conspecific song need not be the same in young and adult birds, or in males and females, nor need the song attributes responded to be the same (Narins & Capranica 1976).

Female zebra finches do not sing and their pathways for the control of learned song are little developed. However, their song preferences can be influenced by experience (Miller 1979*a, b*). These preferences may result from unlearned and learned biases represented in their classical ascending auditory pathway, particularly in Field L and associated neostriatal areas: nucleus interface and the very small HVC (Williams 1985). There are other auditory projections to the telencephalon (Delius *et al.* 1979; Kirsch *et al.* 1980; Doupe & Konishi 1988) and they too could play a role in auditory learning. In males the auditory sensitivity of the ‘motor’ pathways for song control (Williams & Nottebohm 1985) may strengthen and supplement the biases of the ascending auditory pathways. The motor programmes that underly the development of conspecific song may include features (Nottebohm 1972; Price, 1979; Marler & Sherman 1982) that resonate to particular sound inputs and thus enhance recognition and acquisition of the correct model. The main roadblock for understanding vocal learning in birds – or in humans (see Liberman *et al.* 1967; Liberman 1982; Ojemann & Mateer 1979) – may have been the idea that two physically and procedurally separate processes are involved, one dealing with sensory learning, the other one dealing with efferent control. Many of the paradoxes may disappear if perception and production are two closely related states of a same system.

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