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Song learning: the interface between behaviour and neuroethology

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SUMMARY

The high degree of developmental plasticity displayed by the songs of oscine birds makes them appropriate subjects for research on the ethology and neurobiology of vocal learning. Strong individual differences and learned local dialects are common. The readiness to acquire new songs appears to persist throughout life in some species and is restricted to relatively short sensitive periods in others. Learning can occur with remarkably few exposures to song. Mimicry of other species occurs but, given a choice, there is a tendency to favour conspecific songs. Evidence is presented for two kinds of vocal learning, one 'memory-based', the other 'action-based.' Subsong and 'plastic song' phases of motor development appear to be obligatory steps in the ontogeny of learned songs. A case is made that acquisition and production should be viewed as distinct phenomena with different physiological correlates.

Research on behavioural development is closely associated with studies of the physiology of development. The two are mutually synergistic, and the synergism is well displayed in research on song learning in birds. This review of some of the characteristics of avian vocal learning as derived from behavioural studies, indicates lacunae in our knowledge about the ethology of song learning, and suggests how the comparative study of vocal development can pave the way for new insights into the underlying neurobiology.

1. INDIVIDUAL VARIATION AND LOCAL DIALECTS

Oscine song birds possess an exceptional degree of developmental plasticity in all aspects of the process of learning to sing. As a consequence of this, birdsongs display variation at many levels of organization. Individual differences are virtually universal. In every case studied so far, song birds distinguish neighbours individually by voice (Falls 1982). There is much geographical variation; on both a gross scale and at the level of local populations (Mundinger 1982; Baker & Cunningham 1985), song dialects are common. The scale of these local dialects varies enormously, from clusters of a dozen or so birds, as in the indigo bunting (Payne 1982), up to 100 or so, as in the corn bunting (McGregor & Thompson 1988). There may be variation between subspecies in the extent of local dialects, as in the white-crowned sparrow, where the number of individuals in a dialect area may vary from a few hundred in one subspecies to many thousands in another (Baker 1974, 1975; Baptista 1975). Some species display dialects very clearly, and others appear to lack them altogether, already hinting at interspecies differences in some aspect of the song-learning process. Species also differ widely in which attributes of song are stable throughout the range of distribution, and which are variable (Nelson 1989; Nelson & Marler 1989). There is thus ample variation upon which the forces of natural selection can operate, exerting an influence on mechanisms of song ontogeny that, as a result, vary widely between species.

Limitations of various kinds are imposed on the process of song development, both in time, in the kinds of environmental stimulation to which birds are responsive, and in the ways in which they respond to that stimulation. These limitations in turn, although sometimes highly species-specific, are not fixed, but themselves display a degree of ontogenetic plasticity.

2. SENSITIVE PERIODS

No bird species is known that is equally ready to acquire new songs at any phase of its life (Marler 1987). Rather it looks as though there are always one or more sensitive periods. These are phases of life when acquisition occurs more readily than at other times. Often there is a single sensitive period early in life, beginning soon after independence and lasting 4–6 weeks. Examples are the song and swamp sparrow, in which the sensitive period opens at about 20 days and begins to close rapidly at 60 days. There are, however, individual differences, and some male sparrows will learn as late as 200 days old. In general, learning occurs with fewest exposures at the onset and peak of the sensitive period, rather than during its decline. As the sensitive period wanes, songs acquired are also likely to be reproduced in fragmented form, rather than reproduced in their entirety.

Sensitive periods for song learning are not restricted to early life. For example, in the European starling, males do not begin learning songs either from tape recordings or from live tutors until they are about 100 days old. They can still learn at one year, but are also

ready to acquire new songs six months later, both from tape recordings and from live tutors (Marler *et al.* in preparation). Other bird species retain the ability to change their song repertoires up to two or three years of age, (for example, the canary (see Nottebohm & Nottebohm (1978))) and possibly in some species throughout life (for example, European blackbirds and mockingbirds).

Despite the research opportunities offered by this variation in the temporal characteristics of sensitive periods, both between and within species, the physiological correlates of sensitive periods for song learning have been little studied. Some sense of the potential is provided by a study of individual differences in song acquisition in the swamp sparrow, *Melospiza georgiana*. Analyses of steroid levels in blood samples taken every two weeks through the first year of life revealed that the presence of estradiol at significant levels in the blood plasma correlated well with the timing of song acquisition, and did so more closely than levels of testosterone (Marler *et al.* 1987). This was unexpected because testosterone, operating either directly or indirectly, has long been postulated as a controlling factor in post-natal ontogeny of the brain mechanisms assumed to be involved in song acquisition. Furthermore, the correlation with estradiol levels was significantly better in individual swamp sparrows that learned songs well than in those that learned songs poorly. In the swamp sparrow, song acquisition occurs during a brief period early in life (Marler & Peters 1988*a*). Comparative studies of the correlates of song acquisition in species with more extended, or recurring sensitive periods for song learning, such as the European starling, will show whether the relation between learning and estradiol levels is coincidental or general. The precise timing of sensitive periods is not fixed, but is in some degree labile, as a function of such experiential factors as photoperiodic stimulation, or deprivation of access to song stimulation (Kroodsmma & Pickert 1980; Baptista & Petrinovich 1984; Eales 1987). This temporal variability offers further opportunities to determine how closely the timing of learning is correlated with neuroendocrine changes suspected of having causal significance (Nordeen & Nordeen 1990).

3. HOW MANY STIMULI ARE NECESSARY FOR LEARNING?

At the height of a sensitive period, new songs can be acquired with relatively few exposures. In the song sparrow, something less than 400 tape-recorded songs is the minimum needed for learning to occur (Marler & Peters 1987). White-crowned sparrows learn adequately from 120 song presentations over several days (Petrinovich 1985) and European blackbirds have learned from 15–20 presentations on a single day (Thielcke-Poltz & Thielcke 1960). The most striking accomplishment is that of the nightingale, studied by Todt *et al.* (1989) in Germany. Nightingales can learn accurately from 20 song sequences presented during the sensitive period, some from as few as 5 presentations. Especially interesting is the way in which they handle long strings of tape-recorded songs.

Individual male nightingales have a repertoire of up to 200 song types delivered one by one in a fairly regular sequence. Hultsch & Todt (1989) explored whether nightingales are capable of learning strings of up to 60 different songs and reproducing them in the original order. They analysed transition matrices relating the order of songs presented to the order in which they were subsequently produced by the pupil. The results show that the sequencing was indeed retained, but only in sub-sequences of 3–7 songs. After producing such a matched sequence, a bird would then switch to another subset from the original sequence, but taken from some other point.

This behaviour suggests that a male nightingale divides up a sequence into manageable subsets of up to seven songs, perhaps as a strategy for memorizing long sequences. The behaviour is somewhat reminiscent of human word learning, where there is also a tendency to ‘chunk’ long sequences into manageable subsets, although in the nightingale we do not know whether sensory or motor factors are responsible. New assays of vocal learning in birds, which are independent of vocal production, are badly needed.

It should be noted that, during the process of song imitation, songs that are produced are not necessarily veritable reproductions of the models on which they are based. Sometimes segments are deleted. New ones may be invented. Some elements may be modified in the course of motor development by processes of improvisation. One source of discrepancies between models and produced songs is the propensity to break songs into elements and rearrange them in various ways. Recombinations may involve not only parts of the same song, but also of different songs, and these do not necessarily have to be songs acquired at the same time. In the song sparrow, recombined phrases may be drawn from models acquired in different training sessions, separated by intervals ranging from 20 to 150 days. This suggests that acquired songs are not kept apart, but reside in a common store, and hints at the possibility that they are divided into segments before the onset of rehearsal and reproduction (Marler & Peters 1987).

4. LEARNING PREFERENCES

A great variety of sounds can be learned and reproduced by song birds. Some birds are renowned as mimics and will readily reproduce the sounds of other species and even mechanical sounds such as the ringing of a telephone. Among the most famous are the lyrebird of Australia, the mockingbird of North America, the starling (see Hindmarsh 1984) and the marsh warbler of Europe. Marsh warblers are known to mimic up to 76 species, some acquired on the breeding grounds, and others in the winter quarters in Africa (Dowsette-Lemaire 1979). However, only about 5% of song birds mimic frequently (Hindmarsh 1984). If they are given a choice, many birds, although able to mimic a range of sounds, are biased to favour acquisition and production of songs of their own species. Some can do so at their first encounter with them. The neural mechanisms underlying this ability

to discriminate between conspecific and heterospecific songs remain unexplored.

That songs of different species are not equipotential as learning stimuli has been best shown in swamp and song sparrows (Marler & Peters 1988*b*, 1989). Birds were presented with identical sets of tape-recorded songs, including both species. Young males each favoured songs of their own species. This was equally true whether they were taken into the laboratory as nestlings, or brought in as eggs and raised under canaries. Thus auditory experience of conspecific song in the egg is not necessary for this preference to be manifest. Songs that were strong learning stimuli for one species were weak for the other, and vice versa.

It is interesting to note that the preference was weaker in song sparrows than in swamp sparrows, both as nestling-reared and as egg-reared subjects. By using measures of heart-rate change, Dooling & Searcy (1980) found that both young song and swamp sparrows were more responsive to conspecific than to heterospecific songs, but that the discrimination was strongest in swamp sparrows. In some birds social interaction with live tutors plays a significant role in song learning, and may be a prerequisite for learning in some. The song sparrow may prove to be a case in which social interaction has an influence on the choice of models for song learning, further reinforcing a bias that is manifest with sounds of song alone.

By using computer-synthesized songs as learning stimuli, and independently varying different acoustic features, it can be shown that the learning preference of male swamp sparrows is based on syllable phonology (Marler & Peters 1989). Swamp sparrows favour conspecific syllables irrespective of the syntactical patterns in which they are presented. In song sparrows the situation is different. Preferences are based both on syllabic structure and also on song syntax. Several syntactical features are involved, including the number of segments, their internal phrase structure – whether syllables are trilled or untrilled, for example – and such attributes as the tempo in which syllables are delivered. There is no evidence that male swamp sparrows refer to any of these syntactical features in choosing models for song learning.

This is a case where comparative behavioral studies have opened up an area that is now ripe for neurophysiological investigation. The enterprise will be challenging because it is clear that the preferences are not absolute. They can be overridden, by withholding access to conspecific songs, and by exposure to learning stimuli with strong arousal properties, such as a live aggressive male caged in close proximity, which can even be a member of another species (Baptista & Petrinovitch 1984, 1986). There is thus potential plasticity in the manifestation of learning pre-dispositions.

5. TWO KINDS OF VOCAL LEARNING

There is growing evidence of two different processes by which songs can be learned. I shall refer to one as 'memory based learning' and the other, more speculatively, as 'action-based learning'. They are dis-

tinguished by the degree of novelty to the existing repertoire of that learned. In the traditional form of vocal learning, song stimuli that are completely novel to the individual's repertoire are committed to memory, stored and subsequently produced. Production occurs by reference to auditory feedback (Konishi 1965; Marler 1976). The relative and absolute timing of memorization and production varies from species to species (Marler 1987). I am calling this the memory-based form of song learning. It is characterized by the occurrence of acquisition before production.

In the action-based form of song learning the impact of experience is closely associated in time with production. A wide range of variable 'plastic' songs produced by the bird is subjected to a process of selective reinforcement by interactions with other birds. In this case the songs 'learned' are not novel but are already present in the individual's plastic-song repertoire, having been acquired, improvised, or invented previously. At this stage of song development, which may occur long after closure of the sensitive period for the 'memory-based' form of song learning, social experience of particular kinds leads to a reduction of song variability, and eventually to crystallization of those song motor patterns that have been selectively reinforced by 'tutors', either male or female (see West & King 1988). When the tutor is a rival countersinging male, the result can be a match between songs of pupil and tutor (see, for example, Nice (1943); Margoliash & Staicer (1989)) resulting from a different set of processes than those underlying 'memory-based' learning. Virtually nothing is known of the physiological underpinnings of this form of song learning that has, I believe, often been confused with memory-based learning.

6. PATTERNS OF MOTOR DEVELOPMENT: SUBSONG

A distinctive pattern of motor development appears to be unique to birds with learned songs (Nottebohm 1972). They begin with subsong, which is an almost amorphous, soft and rambling twittering bearing little or no resemblance to natural adult song. It is often similar across species. In plastic song, the second stage, species diverge and the first signs of vocal rehearsal of previously acquired song themes become evident, together with themes that the bird has invented. These themes are all over-produced in abundance in plastic song, and then subjected to selective attrition as the time for song crystallization approaches (Marler & Peters 1982*a*).

The timing and nature of the plastic song – crystallized song transition varies greatly between species. In some, such as the zebra finch, all phases of motor development are compressed into a short period early in life, with crystallization occurring early. In others it may be appropriate to view mature singing behaviour as plastic song, with crystallization in the typical sense never taking place. In such species, it may be that the capacity to change song by selective reinforcement, the action-based form of learning, persists throughout life, whenever singing occurs.

Margoliash & Staicer (1989) have suggested that in the Indigo Bunting, which retains some ability to modify song into adulthood, both crystallized song and plastic song persist after sexual maturity, and that preferences among plastic songs are shaped by counter-singing with other males, leading to the incorporation of additional themes into the crystallized-song repertoire.

7. IMPROVISATION AND INVENTION

What kinds of developmental process underlie the highly variable structure of plastic songs? The reproduction of previously memorized songs obviously plays a part. Some of the deviations from precise imitation must be attributable to copy errors (Lemon 1979), but other deviations are clearly imposed by the bird itself. The predisposition to segment learned songs and to recombine the segments to generate new sequences has already been mentioned. This is a widespread means of generating novelty, again based primarily on models acquired earlier in life.

We also see evidence of more creative processes, involving invention and improvisation, their incidence varying strikingly between species. The red-winged blackbird, for example, is a compulsive improviser. During plastic song, a male red-winged blackbird submits acquired themes to continuous experimentation and embroidery, eventually transforming many of them to such a degree that the originals are no longer recognizable (Marler *et al.* 1972).

There are also hints that improvisation and invention are applied more consistently to some segments of song than to others, which are left as pure, unadulterated imitations. Thus in a species like the white-crowned sparrow, it sometimes appears in some populations that dialect characteristics are confined to certain components of the song, with other song segments or features being more free for individual improvisation (Marler 1970). The corn bunting may be a similar case (McGregor & Thompson 1988).

Improvisation-generated cues, encoded in one song segment or feature, may subserve personal identification in many songbirds (Falls 1982). Imitated cues, marking the local dialect, may reside in another, and cues for species recognition in yet another set, with arrangements varying from species to species (Marler 1960). However, these comments on creative aspects of song ontogeny are based largely on anecdote. Such phenomena would repay closer and more systematic investigation, especially as they vary strongly between species. Again, it is a challenge for the neuroethologist to characterize the physiological basis of such species differences in song ontogeny.

8. ACQUISITION AND PRODUCTION AS DISTINCT PROCESSES

The swamp sparrow illustrates another potential of the comparative approach to the study of memory-based song learning. In two of the classical subjects for research on the neurobiology of vocal learning, the zebra finch and the canary, it has been difficult to

differentiate between events surrounding the memorization of songs and those associated with song production because they are compressed together in time (Immelmann 1969; Marler & Waser 1977; Waser & Marler 1977; Nottebohm *et al.* 1986, 1987). In the swamp sparrow, however, as studied in the laboratory, these two phases of memory-based song learning are separated in time (Marler & Peters 1981, 1982*b*). This temporal separation has been exploited to show that the brain is in different states in these two phases of song development (Nordeen *et al.* 1989).

Components of the song system in the oscine brain originally described by Nottebohm and his colleagues (Nottebohm *et al.* 1976) are growing rapidly at the time of song acquisition. This growth, resulting from the process of neurogenesis discovered in the canary (Goldman & Nottebohm 1983; Nottebohm 1985), has almost ceased by the time of song production. The major period of neurogenesis in HVc and area X thus coincides well with the period of song acquisition, but not at all with the period of plastic- and crystallized-song production.

The conception of 'memory-based' song learning as involving at least two distinct processes, memorization, and reproduction, merits closer investigation, implying as it does that the physiological mechanisms responsible may be separate to some degree. Yet another set of processes is presumably associated with 'action-based' learning.

9. THE ROLE OF STEROID HORMONES

An accumulation of evidence indicates involvement of hormonal mechanisms in these developmental transitions. As I have already mentioned, one close correlate of song acquisition but not of song production, in the swamp sparrow, is the presence of estradiol in the plasma (Marler *et al.* 1987, 1988). Note that the focus is on estradiol and not on testosterone, which has often been invoked both as a correlate and a causal agent of song learning. In male swamp sparrows, testosterone levels are indeed elevated at the time of song acquisition, but they prove to correlate poorly with readiness to learn. It has been shown that testosterone is not a prerequisite for song acquisition.

Male swamp sparrows were castrated at 20 days and checked every two weeks to confirm that testosterone was not present in the blood plasma. These castrated males learned songs at the normal time and at normal rates. On the other hand, estradiol was found to be present at normal levels, implying that it can originate from a non-testicular source. The organizational role of estradiol in masculinization of the male song-bird brain was established by Gurney & Konishi (1980), operating around the time of hatching. We may have to consider an additional role for estradiol, operating in a more activational mode, occurring somewhat later in life, at the time of song acquisition.

Testosterone, however, appears to be an active agent in song production. Castrated male swamp sparrows developed both subsong and early plastic song without testosterone therapy, but testosterone was necessary for song crystallization (Marler *et al.* 1988). Thus the

hormonal environments associated with early and late phases of song production may differ. The evidence points to the crystallization of fully mature patterns of song production as a distinct event, with testosterone playing a role in that transition.

10. CONCLUSIONS

Dramatic progress has been made in recent years in analysing the neural and hormonal substrates for vocal learning in birds (see, for example, Bottjer & Arnold (1986); DeVoogd (1986); Nottebohm (1987); Konishi (1989)). Many significant ethological phenomena still remain physiologically unexplored, however. These include sensory and motor mechanisms underlying species-specific learning preferences, neural and hormonal correlates of inter-species variation in the number and timing of sensitive periods for song acquisition, and the possibility that the acquisition and production of a song are associated with different sets of physiological determinants. The hypothesis, derived from behavioural studies, that there are two kinds of vocal plasticity in birds, one memory-based, the other action-based, merits physiological investigation, and may resolve some of the contradictions in the literature about the timing of sensitive periods for song learning. Further exploitation of comparative approaches may be especially fruitful in ensuring that the continued interplay between behavioural and neuroethological investigations of avian vocal learning will remain scientifically productive.

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