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Psychobiological and ecological aspects of song learning and memorization

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ABSTRACT. *Psychobiological and ecological aspects of song learning and memorization.*- This paper deals with some representative findings on the rules of how perceptual experience translates into behavioural performance in the nightingale (*Luscinia megarhynchos*). Some of them point to special process learning (song level), while others (inter-song level) bear striking parallels to rules of information processing found in other biological systems (e.g. capacity constraints during perceptual experience; hierarchical memory organization). In the song acquisition system, these mechanisms interact in a fascinating way, allowing the bird to develop a unique and flexible signalling behaviour.

KEY WORDS. Acquisition mechanisms, Information processing, Exposure variables, Memory, Nightingale (*Luscinia megarhynchos*), Retrieval mechanisms, Serial learning

Introduction

Along with the evolution of song as a culturally transmitted behaviour in oscines, a system of adaptations has been developed to reduce the complexity of a young bird's auditory world and guide the perceptional phase of song learning. These are: A neural predisposition for the acquisition of the species typical song pattern (signal selectivity); a preference to acquire song from a socially significant individual (social sensitivity); and a specification of the timing of perceptual learning during ontogeny (sensitive phase) (rev. in Kroodsma & Miller, 1982; Slater, 1989; Marler, 1991).

There are large differences among birds in the extend to which a given species 'relies' on the one or the other mechanism. Some can be easily trained with heterospecific song patterns, while others fail to imitate them. Some birds can be tutored in the laboratory by playing a tape to them, others need a so called social tutor. And some birds have a temporally quite defined age at which song acquisition occurs, while others may extend learning at least throughout their first years of life (Todt et al., 1979; Payne, 1981; Böhner, 1983; Clayton, 1987; Chaiken et al., 1994; Marler & Peters, 1987, 1988; Baptista, 1990).

Much of recent experimentation on these issues has resulted in a fading of formerly well delimited stats on what is learned, and from whom or when acquisition occurs. And much of its fascination comes from discoveries on the intricate tuning of mechanisms to the particular niche related problems a species or even a population encounters. There is a problem common to most oscines: a young bird set out to acquire its species song is exposed to stream of physically most volatile information about complex stimulus configurations and successions. This points to another set of adaptations, i.e. those associated with the question how to learn. Such a question addresses the properties of specific processes involved in the song learning such as perceptual acquisition or the storage and retrieval of acquired information. The present paper focusses on this facet of the song acquisition system.The non-invasive, behavioural approach for elucidating these processes is to study, and finally make inferences from the analysis of input - output relationships. And, the basic task for the experimenter is to describe in detail the systems properties, that is its specific capacities and constraints.

My paper will deal especially with such psychobiological aspects of song learning and song memorization. Ecological aspects of these matters will be treated marginally. Concurrently, I will concentrate on a model species, the European nightingale (*Luscinia megarhynchos*). It has three crucial properties: First, the birds acquire many different types of songs. This has a number of implications for setting the framework for experiments on the system's capacities and constraints. For example, it allows to extend the examination of effects to the inter-song level and ask questions on whether learning affect song-type sequencing. Second, the birds accept a standardized playback learning design. This allows elegant experimental access to the variables involved in their learning accomplishments. For instance, does exposure frequency to stimuli have implications on acquisition success? Third, the birds show high vocal activity, i.e. they perform developed songs frequently enough to assess rules of song organization and, based on this, to infer on the rules of the acquisition and memorization processes. The following chapter will outline some general aspects of the nightingales' singing behaviour.

Material and Methods

Nigthingales as a candidate species

The nightingale (*Luscinia megarhynchos*) is renowned for its vocal virtuosity. Hultsch (1980, 1981) distinguished several structurally different forms of singing which covary with singing context. These are nocturnal singing, chorussing, (advertising singing, countersinging and courtship singing.

Nocturnal singing is characterized by the following features: Singing periods have a long duration, often lasting for several hours. Song-type sequencing is more versatile, sylable repetition in trills is more extended and the performance of a special song category ('whistle songs') is more frequent than during other times of the day. Finally, as a rule, birds do not change song posts in the dark. Nocturnal singing begins some nights before the arrival of females and lasts for a period of about three weeks. It is supposed that it is involved in attracting the nocturnally migrating females and in supporting their stay until they become territorial (Hultsch, 1980, 1981).

During chorusssing which begins about one hour before sunrise and lasts for ca 40 min, nightingales modify their singing style as compared to the nocturnal singing, namely by briefing the trill section of songs (Gamma sections) and especially by reducing silent intersong intervals from about 4 s to about 1.5 s (Hultsch, 1980; Hultsch & Todt, 1982).

Advertising singing is the least versatile of all singing: Short songs are performed in 'sequential loops'(e.g. : A, B, A, C, B, D, C, B,..., Capitals =

song-types). Although there is low song-type versatility, transition versatility in the performance is nevertheless high. This singing is given during full light, predominantly from exposed perches and may be interrupted when an established neighbour starts singing . As a territorial display it can clearly be distinguished from countersinging. Countersinging is a subcategory of vocal interactions in songbirds. It includes a number of responses evidenced by time specific (e.g. temporal adjustment of intersong intervals either by very precise leader/follower song onset latencies or by overlapping latencies) or pattern specific relationships (e.g. vocal matching, convalent replies, song-type switching) among signals. During night, versatility during countersinging is lower than during nocturnal solo singing. This is mainly due to series of 'to and fro' responses exchanged between males. During daytime, countersinging occurs at territory boundaries or during close distance interactions with intruders, i.e. mainly early in season (Todt, 1971a).

During courtship singing, no specific song-types are used. Nevertheless, it sounds different as compared to the other singing forms . Short songs are delivered in soft voice and with extremely short intersong intervals (around or shorter than 1 sec. as compared to about 3-4 sec.). Song reduction comes from a shortening or complete omission of the trill sections of songs. So, about two thirds of a song is made up by the note complex preceding the syllable repetitions of the trill section. This, together with the dense delivery, makes this singing form sound 'complex' and strangled to our ears.

Tutor singing is uttered by males a few days before and for about two weeks after fledging of their young. Normally, it precedes or follows a feeding act in a distance of about five meter from a young's position (field observations) Bouts are short, comprising five to ten different song-types. Duration of songs and intersong-intervals are of average duration (ca 3s or 4s, respectively).

In Central Europe, nigthingales hatch by the end of May and leave the nest about two weeks later. Their early sensitive phase of song acquisition starts around day 15 posthatching and lasts at least throughout the first three months of life (Hultsch & Kopp, 1989). Within this phase each individual bird can acquire many different types of song. Thus young males are endowed with basic information for the development of their large vocal repertoires (in adult males it may comprise more than 200 song-types; Hultsch & Todt, 1981) before leaving their natal sites for winter migration.

As with many other oscines, social properties of learning contexts affects the song acquisition of young nigthingales. In a choice design (Todt et al., 1979) they readily learn species specific songs presented by a life tutor, but neglect such songs if they hear them when the tutor is not present. In the field, the tutor role is probably taken by the birds' father who frequently interacts with them, e.g. by feeding. In the laboratory, prerequisites of tutor acceptance are bird-tutor interactions, and also the age of birds when interactions begin. In contrast, the biological properties of a tutor seem to be less important. As young bull finches (*Pyrrhula pyrrhula*; Nicolai, 1959), nightingales learn songs from a human being provided he has hand-raised them from day 6 post hatching on (Freyschmidt et al., 1984). Basing on this, experimental settings have been developed for the training of young nightingales, in which variables of exposure can be easily controlled and standardized through a play-back tutoring with tape recorded songs. Normally, in this setting the birds have visual contact to the tutor who visits them with a loudspeaker through which a selected list of tape recorded songs is played back (Hultsch et al., 1984).

The social selectivity decreases later in life. Experiments conducted when birds had reached an age of about 9 months showed that males are able to acquire new songs heard from tape alone (Hultsch, 1991a). This is roughly the time, when free ranging

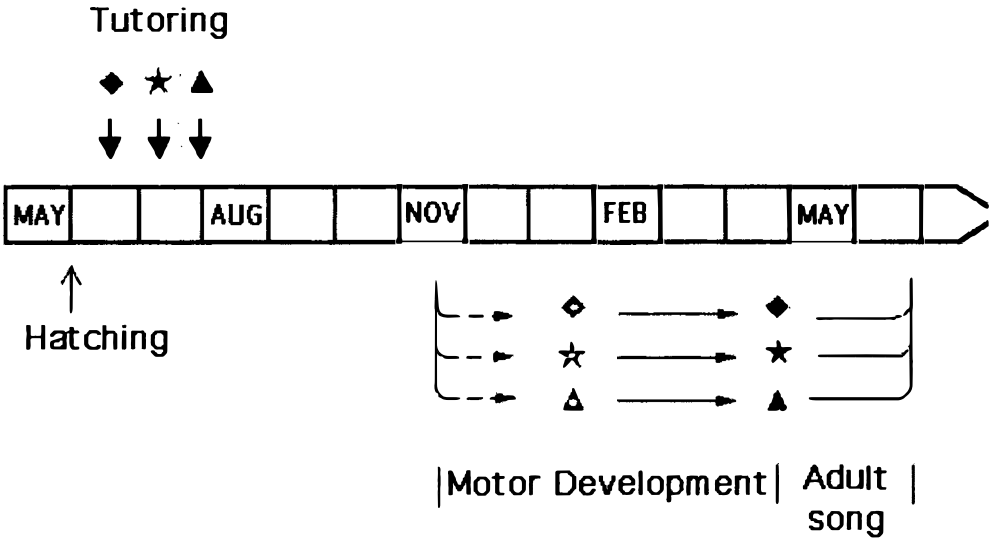


FIGURE 1. Calendar of the first fifteen months in a nightingale's life. Early in life, males are exposed to tutoring programs from which they acquire their songs. Typically, by the end of January, song precursors develop and their crystallization takes place by the end of April. Symbols refer to master song-types (left) or their imitations.
[Calendario de los primeros 15 meses de la vida de un *Luscinia megarhynchos.*]

birds may have access to further exposure to conspecific songs in their winter quarters (J. Nicolai, pers. comm.). As recently shown, the decrease in selectivity is due to previous auditory experience with conspecific model songs and not a mere consequence of age (Todt et al., 1979; Todt & Böhner, in press).

In nightingales, there is a long span of time between the phase of auditory learning and the onset of song production or motor learning (fig.1). Normally birds remain silent during that time. In November male birds begin to produce the so-called subsong. It is made up by 'amorphous' vocalisations. The role of subsong in the song acquisition of oscines has not yet been approached experimentally. It is proposed that it is involved in developing the neuromuscular coordination of the vocal apparatus (Marler, 1991). After a short winter hiatus, first but still very crude imitations can be discerned in January. During the next three months, the motor development of song proceeds through several stages of plastic song. Approximately by the end of April the sensori-motor phase of song development is completed: Songs are stereotyped in phonology and syntax and successive songs are spaced by the typical intersong intervals. After the summer moult, there is a regression to plastic song (PM song; Lange, 1987) and seasonally during springtime, before each period of crystallized singing in the adult birds. The reference of the following chapters is the crystallized, adult song of the first year birds, performed for a period of about two months, that is until late June.

Methodological Procedure

In the experiments reported in this paper, the song-types to which birds get exposed are normal, species typical song-types drawn from performances of free ranging males. Such song-types become members of our catalogue from which they are selected at random and recordedon tape to form a particular string of master song-types (= model songs). The catalogue (currently with 214 song-types) contains model songs only that had been tested in former experiments and were found to (a) be equally good for acquisition and (b) not occur in a birds repertoire if it has not been presented during the tutoring. In the standard design, the duration of intersong intervals separating successive songs is 4s. Tutored song strings presented in the standard design have three properties in common. First, each model song in a string is a different song-type and, likewise, each of the different strings to which a subject is exposed during the period of tutoring, consists of a unique set of song-types. This means that song-types occuring in one string do not occur in another one. And, second, birds do not have auditory access to any of the master song-types outside a specific set of training sessions.

By using particular sets of learning stimuli in a particular learning situation or tutoring regime, we arrive at labelling that situation or regime. And, this in turn, allows inferences on whether and how a particular exposure variable had influenced the singing of the tutored subjects. The first step in the analysis of the developed song patterns developed consists in the checking for imitations of master song-types presented during the tutoring. Normally, the structural details of models are quite faithfully copied and deviations concern mainly additions or

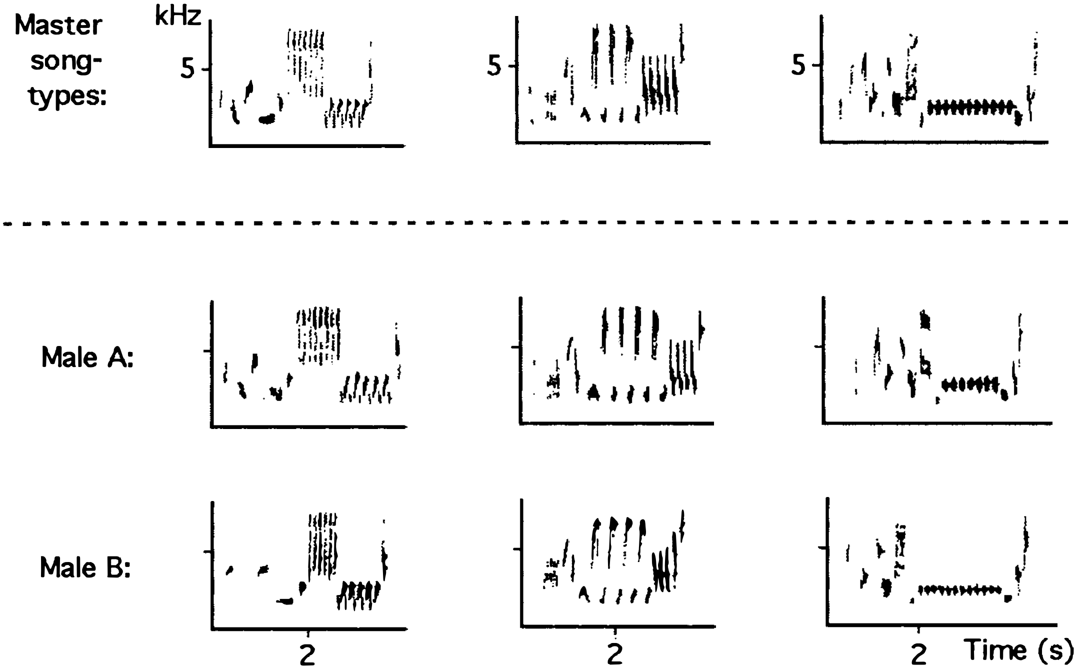


FIGURE 2. Spectograms of three different master song-types (top) and their imitations developed by two males (bottom).

[Espectrogramas de tres diferentes sonidos-tipo maestros (arriba) y sus imitaciones desarrolladas por dos machos (abajo).]

deletions of some syllables in the first song sections. Hence, the identification of imitations is quite straightforward and, as a rule, unambiguous in nightingales (fig.2).

The next step is to relate both the acquired song-types and the mode of their performance to variables that may have affected acquisition succes. Such variables can be distinguished as 'biological' in the broader sense, or 'experimental' variables. Some of the biological variables, such as species specificity of presented song patterns , age, experience and relation to a given social context have been mentioned beforehand. Others are, for instance, state and motor deveplopment. Experimental variables, on the other hand are, for instance, features of the tutoring regime, such as exposure frequency, string length, presentation rate, serial position and the distribution of tutoring sessions in time. The exploration of these varibales plays a crucial role in addressing questions on the capacities and constraints related to the memory for song patterns.

Results

Acquisition success on the level of song patterns

For the song acquisition of versatile songsters, like the nightingale, two questions arise. One concerns the acquisition of information encoded in the patterning of songs, that is in the within-song phonology and syntax. The other one addresses the acquisition of information encoded in the succession of song patterns or the between-song syntax. A study of the first issue focusses on the variable acquisition success given by the relation of acquired songs versus presented model songs, and may include the 'copy quality' of acquired songs. In this chapter I will outline whether and how acquisition success is influenced by specific experimental variables, namely exposure frequency, string length, distribution mode of master song-types and their presentation rate.

Exposure frequency: In a classical experiment on the song learning of birds subjects hear hundreds of renditions of a song pattern. There are mainly logistic reasons for doing so, for instance, one wants to make sure that the particular research objective is not thwarted by too few exposures. If, however, one wants to examine the influence of presentation frequency, one should find out critical boundary conditions where this variable may become a constraint on the aqcuisition of stimuli. Analysis of the birds' acquisition success revealed two results (fig.3). First, about 20 to 40 percent of song-types which subjects experienced only two, or five times were acquired. Second, there was a marked increase in acquisition success with more frequent exposures, but this leveled off beyond a ten times exposure.

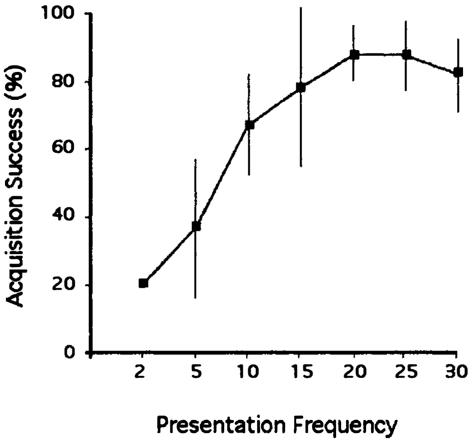


FIGURE 3. Presentation frequency of master song-types plotted against acquisition success. (M, SD).
[Representación de freciencias de los sonidos-tipo maestros frente al éxito adquirido.]

Temporal distribution of trials: This means that the presentation of learning stimuli can follow either a temporally distributed or a temporally clumped regime. For example one can play a song string once per day on twenty successive days and consequently distributed in time. The equivalent in a clumped exposure is to play that string twenty times on one day only. It is a known fact from other fields of learning research that a distributed regime of trials facilitates the acquisition of a trained task as compared to clumped exposure (c.f. Crowder, 1976). In the nightingale experiments this variable did not result in differences in acquisition success.

String length: It stands for the variable 'number of songs', here. One can increase string length from ten, to thirty or 60 song-types without increasing exposure frequency beyond 20 times. The birds coped well with such increase in the amount of stimuli to be acquired. This finding contrasts with empirical generalizations from learning theory saying that exposure frequency has to grow proportionally with the amount of learning stimuli to be acquired (c.f. Crowder, 1976).

Presentation rate: It means the number of songs heard per unit of time. The acquisition success was highest with playing 10 songs per minute, which corresponds to the normal, species typic singing rate. Interestingly, both a shortening of intersong intervals down to 1s and a prolongation of pauses to 20s resulted in a lowered acquisition success (Hultsch, 1992). This effect may be accounted for by an adaptation of the system to a biologically significant rate of input.

Such idiosyncrasies of bird song learning bear directly on the issue of song acquisition as a special process or template learning. In proposing a neuroselectional model of the song acquisition system, Marler and Nelson (1992) recently argued that genetically preordained information about song phonology and syntax does not only act as a neural filter for selective attention to the species song but, in addition, is directly involved in the process of stimulus memorization. From the neuroselectional point of view, a heard song pattern would somehow exert an activating influence on this precoded information, rather than being the material which has to be memorized. The neuroselection hypothesis may account for the astounding low frequencies of exposure to model song-types sufficient for their imitation. However, a model heard five times is less likely to be imitated than a model experienced, for instance, 20 times (c.f. fig.3). Therefore, it could be that exposure frequency has some incremental effect of activation in the template system.

Taken in its strict form, the hypothesis predicts that exposure frequency (low or high) to a given model would not affect the 'quality' of the mental image of that model. One may indirectly address this issue by examining the copy quality of developed imitations. It was measured in a score of low, medium and high, which takes into account both syntactical (e.g. syllable deletions, substitutions) and phonological variables (acoustical Gestalt). The comparison of imitations revealed that imitations from low frequency exposure were significantly more often in the category 'low quality' than those from high frequency exposures. In addition, the copy quality of the latter was frequently scored as 'high quality' (fig.4). Such positive relationship between exposure frequency and copy quality allows to infer that more frequent exposures to a model mediate a better store. But, similar to the effects of exposure frequency on the probablity of imitation, the distribution points to a satiation of this effect at remarkably few exposures already.

The point which emerges from these analyses is that any examination of memory mechanisms in the song acquisition of birds has to take into account that genetic guidelines are involved in the process, be it in identifying appropriate models for learning and/or in directly mediating their quick memorization. And one alley of future experimental research would be to specify their contributions as process variables.

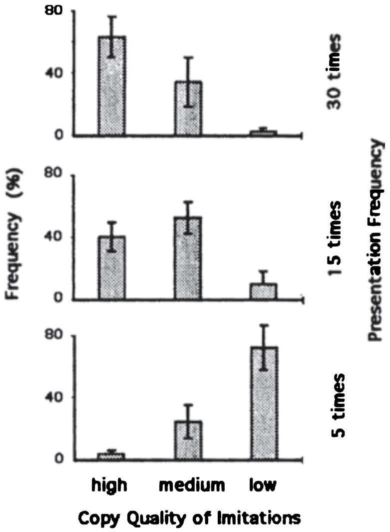


FIGURE 4. Copy quality of imitations developed from master songs that had been presented for different number of times during the tutoring.

[Cualidad de la copia de las imitaciones realizadas de los sonidos maestros que se presentaron diferente número de veces durante los experimentos.]

Information encoded on the level of song-type successions

From the way the tutoring is conducted (c.f. methods) one arrives at labeling the following two levels of pattern sequencing: the succession of master strings during the period of tutoring and the succession of song-types that make up a given master string (fig.5). With this is a reference it was examined whether nightingales would acquire information about the succession of different master strings. If this was the case, birds successively exposed to e. g. five different strings would produce imitations of master songs in a way similar to the order of string succession. Sequence analysis with imitations labeled according to the particular master string from which they had been acquired, revealed no indication for such a performance organization.

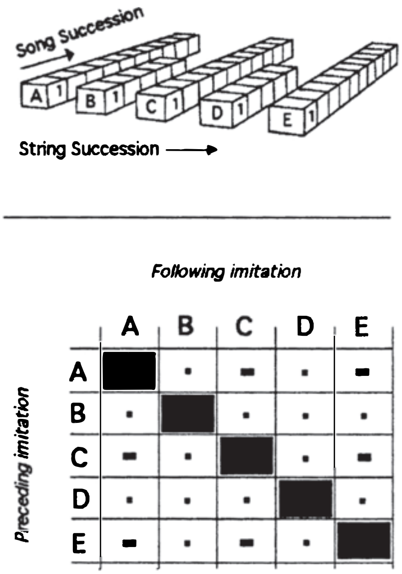


FIGURE 5. Top: different levels of pattern sequencing during the tutoring with bars representing different master strings. Bottom: schematic illustration of the 'Context Effect' in a transition matrix. Symbols for the tutored strings (capitals) are given in the row and column categories. The hatched areas in the cells of the matrix body represent transition frequencies between the developed imitations (here classed only as developed from a given string).

[Arriba: Niveles diferentes de secuenciación de pautas durante el experimento de tutoría con barras qe representan distintas cadenas maestras. Abajo: Ilustración esquemática del “Efecto Contexto” en una matriz de transición.]

However, the birds' singing clearly showed another phenomenon, termed 'Context Effect' (Todt & Hultsch, 1989a) and illustrated in fig.5: Imitations acquired from a given string of model songs were performed in sequentially coherent bouts, i.e. they are seggregated from imitations of models acquired from another string. This indicates that the birds acquire categorical information such as 'member of the same string'. They store this information over a period of almost a year and refer to it in the organisation of their own singing.

The second question was whether nigthingales would acquire information encoded in the serial succession of model songs that make up a given master string (fig. 6). If this was the case one would predict that the succession of imitations would match that one of the master songs. Here, the analysis provided a positive answer. Birds indeed prefered to sing those imitations successively whose models they had heard successively, but such transition preference covered a considerable span of both forward and backward transitions. So, the birds had acquired serial information, but they seemed to have stored information about the sequential neighbourhood of model songs.

Is such a 'Neighbourhood Effect' due to constraints in the acquisition of serial information, or does it reflect an organizational format of how the sequence is represented in the bird's brain? These matters have been examined by allowing nigthingales to hear different strings for different numbers of times.

For increased exposure frequencies the results revealed a clear relationship between presentations and the reproduction of serial order. It was remarkably better when the birds - instead of hearing a master string only 25 times - heard it 50 or 100 times. This phenomenon was called 'Serial Order Effect', a term borrowed from studies on human serial item learning (Hultsch and Todt, 1992a). However, even with a 100-times exposure, there persisted some sequential noise due to transitions to more 'distant' imitations. There are feasible reasons to interprete the noise as an inherent property of the system (see below).

The other set of experiments tested whether reduced frequencies of exposure would allow to characterize boundary conditions where exposure would become a constraint in the acquisition of serial information. In designing such experiments one has to take care not to lower stimulus presentations to a degree where constraints in pattern acquisition come into play (c.f. page 7). Therefore, exposure frequency to songs was kept in the normal range (15 times). But the serial succession of song-types in a string was randomized anew and rearranged after a preset number of subsequent exposures. So, while birds heard any song-types 15 times, they were presented only for a particular

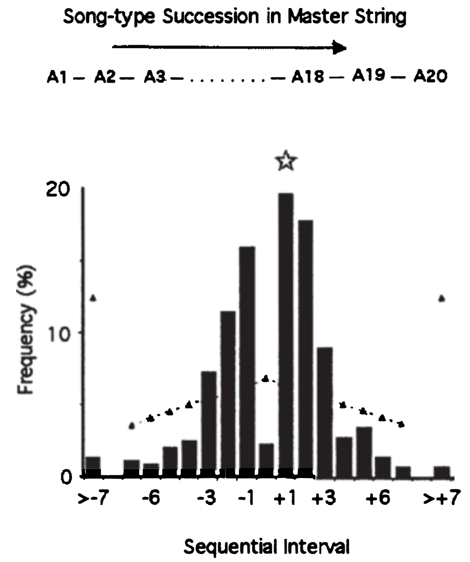
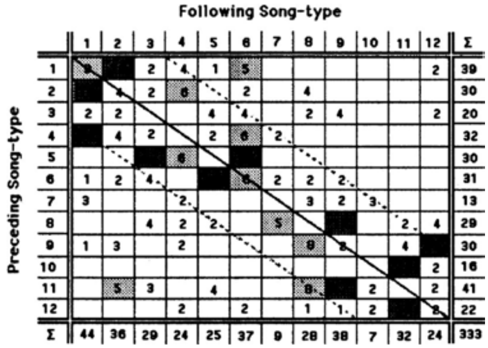


FIGURE 6. Frequency distribution of sequential intervals observed for transitions between any two successively performed imitations developed from a tutored master string (string length: 20 song-types, presentation frequency: 25 times). Sequential intervals refer to the succession of master song-types in the tutored string. Entries to the class labeled by the star (+1) refer to transitions which matched the serial order of master song-types. The remainder positive intervals refer to transition steps 'forward', the negative ones to those 'backwards' in the sequence. Marginal columns give data pooled from entries to the interval classes -7 to -19 or +7 to +19, respectively. Entries to class '0' give repetitions of a song-type. Triangles give expected transition frequencies on the basis of a random succession of imitations. Data pooled from 6 males.

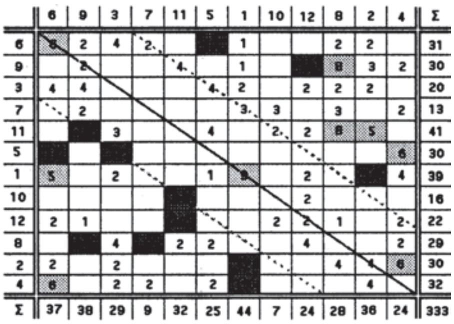
[Distribución de frecuencias de intervalos secuenciales, observados para transiciones entre cualquier par sucesivo de imitaciones, realizadas de una cadena maestra.]

First Sequence Version:



	1	2	3	4	5	6	7	8	9	10	11	12	Σ
1	[illegible]	■	2	4	1	5						2	39
2	■	4	2	6		2		4					30
3	2	2			4	4		2	4			2	20
4	■	4	2		2	6	2						32
5			■	6		■							30
6	1	2	4		■	[illegible]	2	2	2				31
7	3			2				3	2	3			13
8			4	2	2		5		■		2	4	29
9	1	3		2				8	2		4	■	30
10											■	2	16
11		5	3		4			8	■	2		2	41
12				2		2		1	1	2	■	2	22
Σ	44	36	29	24	25	37	9	28	38	7	32	24	333

Last Sequence Version:



	6	9	3	7	11	5	1	10	12	8	2	4	Σ
6	[illegible]	2	4	2		■	1			2	2		31
9		2			4		1		■	8	3	2	30
3	4	4				4	2		2	2	2		20
7		2					3	3		3		2	13
11		■	3			4		2	2	8	5		41
5	■		■									6	30
1	5		2			1	[illegible]		2		■	4	39
10					■				2				16
12	2	1			■			2	2	1		2	22
8		■	4	■	2	2			4			2	29
2	2		2				■			4	4	6	30
4	6		2	2		2	■				4		32
Σ	37	38	29	9	32	25	44	7	24	28	36	24	333

FIGURE 7. Illustration of the 'Primer Effect'. Cells give transition frequencies between imitations developed from a master string in which the sequencing of model songs was rearranged upon every string presentation. The succession of master songs (here labeled by numerals) is given in the row and column categories of the transition matrix. Top: arrangement according to the first presented sequence version. Bottom: arrangement according to the last version. Numbers in the matrix body are transition frequencies between imitations observed in the singing of one male. The data show that the sequencing of imitations gave a good match to the first sequence version only.

[Ilustraci6n del "Efecto Cartilla".]

number of times to a given song-type succession.

The experiment allowed not only to assess critical exposure frequencies for the acquisition of serial information. If birds would cope with this design, the labeling of exposures would permit to find out from which string version the acquisition took place. The analysis provided two results: First, the birds had acquired information encoded in the first sequence version played to them. In contrast, the birds' singing did not give any indication that serial information from other sequence versions (incl. the last one) had been acquired. Second, a single exposure was sufficient to make singing non random with respect to the song-type successions of the first sequence version (fig. 7). This finding has been termed Primer Effect (Todt & Hultsch, in prep).

The stable exposure related sequential neighbourhood of acquired imitations in the birds' singing raises questions on the coding format of serial information in their memory. Theoretically, there are two possibilities of how this matter can be conceived. It could follow a Markovian model (every item or song-type is associated with any other one; strong associations between adjacent, weaker associations among sequentially more distant items). Or it may be hierarchical due to a distinct clustering of associations only among particular items. The analysis confirmed the hierarchical model. Its expression has been termed Package-Effect (Hultsch & Todt, 1989b).

In functional terms, the lable Package-Effect describes the fact that a larger body of serial data, here information from a string of master songs, is segmentized into subsets of sequentially associated items. Such associations have a number of characteristics. The most striking features are (1) bidirectional or multidirectional of associations among distinct sets of aquired song-types and (2) the limited size of song-type packages: Distributions of package sizes revealed a prominent peak between three and five song-types.

Discussion

This paper addressed some representative findings on the rules of how perceptual experience translates into behavioural performance in the nightingale. Some of them point to special process learning (intra-song level), while others bear striking parallels to rules obtained in other fields of research on serial learning. In the song acquisition system, these mechanisms interact in a most fascinating way, allowing the bird to develop a unique and flexible signalling behaviour (Hultsch, 1991b). The emphasis of this final chapter will be on results obtained from analyses on the inter-song level and to discuss implications for the acquisition and memory mechanims.

The findings allow to distinguish three kinds of associations among acquired serial information: the songs (as associations of syllables or motifs), the song-type packages and the context groups. Songs and context groups clearly reflect the organization of the input during auditory learning. Therefore both are regarded as exposure induced pattern associations. Concurrently, however, they differ in a basic characteristic: Whereas the structure and length of songs are constrained by species specific factors, context groups are both variable in structure and size. Moreover, context groups are 'open' to the addition of new song-types. This has been evidenced in experiments where new song models were appended to master strings which the birds had already experienced as fledglings. Birds who heard these strings in their first spring acquired the new song-ytpes and constistently performed the imitations as members of the 'original' context group (Hultsch, 1991a).

Different from the context groups, the package groups can be characterized as 'closed' pattern associations. That is, further exposure to new song models (c.f. last para) resulted in the formation of new packages, rather than in a modification of already existing ones. In addition, they are self-induced 'chunks' of information. On the basis of a hypothesis on package formation, the latter was predicted as the result of a process which segments information about song-type successions which was temporally coherent upon exposure. Theoretically, such a segmentation process could be part of either acquisition processes, the storage system, or it occur upon the retrieval of stored information. From the experiments carried out to date there is at a quite fair network of evidence supporting the hypothesis that package formation is due to a process which segments serially presented information already during auditory acquisition. The examination of this issue suggests that segmentation ensues from short term memory mechanisms with dual constraints. These are (1) a time constrained memory span (max. 55s) during which the data of perceived song-types are retained on a particular level of processing or analysis and, (2) an information constrained capacity buffer which allows acquisition of a limited number of units (max. 7 song-types) (Hultsch, 1992).

The paradigm of package formation has suggested a number of experiments to further specify the acquisition process. Those which had been carried out to date have supported the properties of the postulated acquisition mechanisms. There are feasible reasons to suggest that also the further processing of data on song-types is packagewise and, above all, takes place as a parallel processing. This would explain, for instance, that for song acquisition to occur, a larger amount of heard songs has not to be compensated for by higher exposure frequencies to these stimuli as e.g. in human serial item learning (c.f. page 8). The evidence further suggests (Hultsch, 1993) that the storage format of serially heard information is hierachical (fig. 8) . In other words: the bird's memory does not only hold information on the song patterns. On a higher level data on song-type packages are represented, and on the next level those of context groups. It is open to date how such hierarchical representation format is

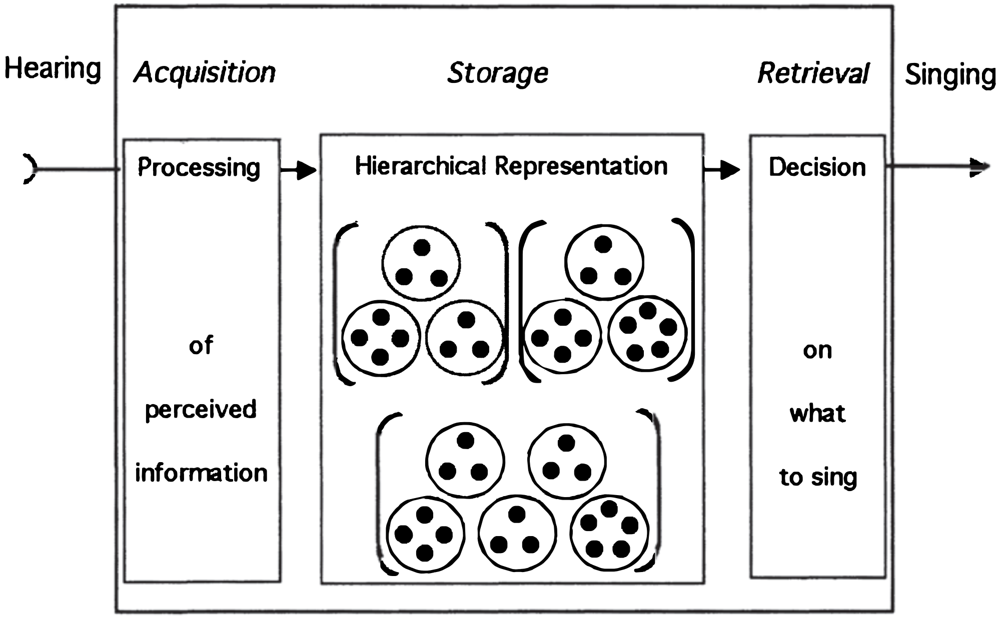


FIGURE 8. Illustration of the hierachical representational format of stored song data inferred from the relationships between organization of learning programs and singing performance. Filled circles: song-types; thin circles: song-type packages; bold circles context groups.

[Ilustraci6n del formato de representaci6n jerárquico de almacenamiento de datos sonoros, inferido a través de las relaciones entre la organizaci6n de los programas de aprendizaje y la realizaci6n del canto.]

realized in the bird's brain (Konishi, 1989; Nottebohm, 1993).

The storage format has, as I presume, a direct relationship to the retrieval of stored information. And with this matter, functional implications arise. One domain concerns the economic and quick access to that information when it is actually translated to vocal signals during communication. In a prestructured repertoire like this, centrally or auditorily mediated decisions involved in determining 'what to sing next' would not have to be made among the whole pool of, say, 100 song-types. Rather, both decision steps and decision time would be reduced by addressing a particular subset of patterns only (Todt, 1971a; Todt & Wolffgramm, 1975). The other domain directly relates to the functional significance of a context related storage of song patterns. The vocal reproduction of groups of song-types heard in a particular tutoring context is likely to have implications for making song delivery an effective signalling in intermale communication. In the experiments reported here, a tutoring context was characterized by a temporally close succession of master song-types (Hultsch & Todt, 1992b). If the system's ability to memorize and store such information is used to associate it with other variables, for instance social or spatial ones, then a whole array of functional implications comes up. Context groups could be conceived as equivalent to subrepertoires, i.e. as ecologically and socially relevant units of storage and retrieval (Hultsch, 1985).

In the field, such a subrepertoire may a set of song-types acquired from of a particular neighbour, or during a particular interaction. The potential to acquire new acoustic patterns and the potential to associate them with patterns that had already been learned as a context related song set, makes the context specific storage a candidate mechanism to facilitate vocal interactions between males (Todt, 1972; Hultsch & Todt, 1981,1982).

Resumen

Aspectos psicobiológicos y ecológicos del aprendizaje y memorización del sonido.

El sistema del aprendizaje del canto de las aves canoras muestra una especialización en la memorización selectiva, con alta capacidad y a largo plazo, de señales a las que las aves se exponen normalmente al principio de su vida. En este trabajo se tratan las propiedades específicas de este sistema de aprendizaje, especialmente de las reglas del procesamiento de información en el "inter-song level".

Las investigaciones se realizaron con ruiseñores (*Luscinia megarhynchos*). La organización del canto de los adultos (de aproximadamente 11 meses) se comparó con la organización de los programas de aprendizaje a los que habían sido expuestos como volantones (de aproximadamente 2-7 semanas). Los resultados de estas investigaciones muestran que hay dos tipos de reglas del canto: primero, las que reflejan informaciones contenidas en los programas de aprendizaje como el "tutoring context", la sucesión y la estructura de los "master songs" (exposure related rules) y segundo, las que reflejan una organización del canto generada de una manera autónoma (song-type packaging).

Estos descubrimientos llevaron a experimentos para investigar los mecanismos que controlan la adquisición y memorización de informaciones seriales, obteniéndose las siguientes conclusiones: (a) Las señales adquiridas por las aves son procesadas como "chunks" de información. El "chunking" es causado por dos mecanismos (time window y unit capacity) que cortan en segmentos las informaciones seriales. (b) Los experimentos de aprendizaje muestran que la primera exposición es de particular importancia para la adquisición de información serial. Los exposiciones siguientes fortalecen esta información. (c) Mientras que la audición y el canto funcionan de una manera serial, la memoria que está interpuesta entre estas dos funciones, almacena informaciones de forma jerárquica.

Este tipo de organización de la memoria, podría explicar la eficacia sobresaliente del procesamiento y del almacenaje de información, en el aprendizaje del canto. Además podría ser el mecanismo que controla el canto de especies que tienen un repertorio amplio y estilos de canto muy versátiles: La reclamación rápida de información de la memoria durante el canto podría funcionar de la misma manera jerárquica, manejando grupos enteros de estrofas (en vez de estrofas individuales).

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